

EARLY ORDOVICIAN TRILOBITES NORA FORMATION, CENTRAL AUSTRALIA

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ABSTRACT. This is the first detailed account of the trilobites from the platformal carbonate/clastic Nora Formation of central Australia. The fauna records a remarkable, endemic radiation of the Family Asaphidae, producing forms with inflated, tuberculate frontal glabellar lobes unlike any other asaphids, but with a general resemblance to certain unrelated trilobites which lived in former epeiric habitats. The fauna is probably of mid-late Arenig age. The generic composition indicates that Australia lay in equatorial latitudes during the early Ordovician, attached or close to the Gondwanaland of the time and well-removed from other continents spanning the palaeoequator. The fauna includes eighteen species, of which four are left under open nomenclature. The concept of the Leiostegiidae is reviewed to include *Aunamitella*, formerly regarded as a bathyurid. The classification of trinucleine trilobites is briefly reviewed. The peculiar blind trilobite *Prosopiscus*, hitherto considered an aberrant cheiruracean, is reclassified in the Phacopina, and for its reception a separate family, Prosopiscidae nov., is proposed. The following new taxa are described: *Aunamitella strigifrons*, *A. brachyops*; *Norasaphus*, *N. (Norasaphus) skalis*, *Norasaphites*, *Norasaphus (Norasaphites) monrocae*, *N. (N.) vesiculosus*; *Lycophron*, *L. rex*; *Fitzroyaspis irritans*, *Hungioides acutinasus*, *Nambeetella embolion*, *Gogoella brevis*, and *Prosopiscus praecox*. On the basis of the trilobite fauna two assemblage zones are defined in the Nora Formation.

THE trilobites described here were collected from the Nora Formation during 1976. Although the formation has a wide geographic distribution (text-fig. 1) extending over at least a 300 km east-west belt, we have restricted our present investigations to the faunas of the Toko and Toomba Ranges, respectively the eastern and western limbs of the Toko Syncline. This area has been more thoroughly documented by members of the Australian Bureau of Mineral Resources Georgina Basin Project than the sequences of either the Tarlton or Dulcie Ranges to the west; the formation is thought to be most completely developed in the Toko Syncline where its stratigraphic relationships are better known, and the trilobite faunas are more prolific.

During the Arenig the continental interior of Australia was immersed beneath a shallow, tropical sea, which supported a rich fauna of trilobites, brachiopods, and molluscs. Outcrops of rocks of this age are widely distributed in the Georgina and Amadeus Basins, but their inaccessibility has meant that the faunas have only recently been studied in any detail. Platform faunas of this kind are relevant to the assessment of the paleogeographic position of Australia during the early Ordovician. This paper describes the trilobite fauna of the Nora Formation, which crops out along the southern margin of the Georgina Basin, central Australia. The fauna is of particular interest because it records endemic morphologies arising within what was evidently a short time; probably no better example exists of the adaptability of the trilobite exoskeleton in the epeiric habitat.

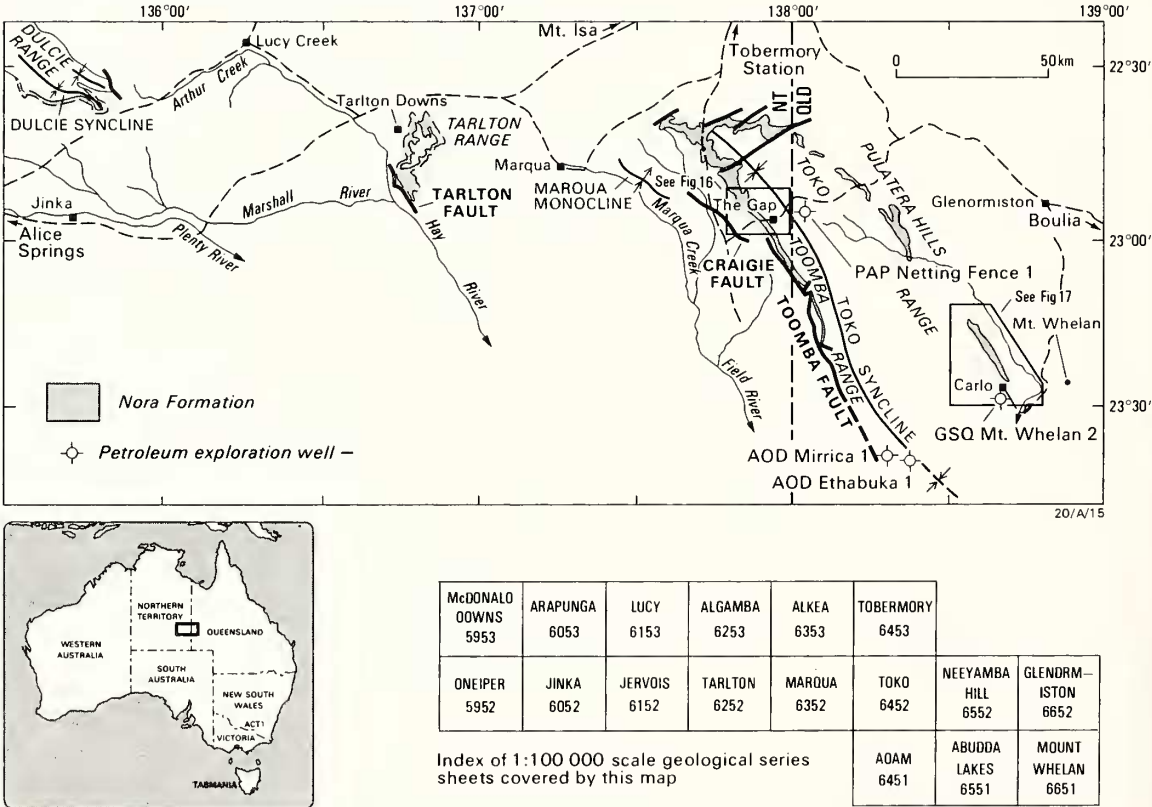
Type material described here is prefixed CPC, and is deposited in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia. A representative non-type suite of material is deposited in the British Museum (Natural History), London, and is prefixed BM It. R. A. F. contributed pp. 318-360, although joint responsibility is accepted for the scientific content of the paper.

STRATIGRAPHIC SYNOPSIS

The Nora Formation was named by Casey (*in* Smith 1963a, p. 10, table 1) for the informally designated rock unit 01-8 of Pritchard (1960, pp. 112-113). Originally referred to the Toko Series (Whitehouse 1936) or Toko Beds (Casey 1959; Pritchard 1960), the Nora Formation is now

recognized as the basal formation of the Toko Group, as revised by Draper (1980, pp. 473–474) who also illustrates the historical development of nomenclature for these rocks. Stratigraphic relationships are illustrated in text-fig. 2. The type area of the Nora Formation is in the northern continuation of the Toomba Range, in the vicinity of Halfway Dam (text-fig. 16), 71 km south of Tobermory. A type section has never been defined. In its type area the formation consists of brown ferruginized coquinite at the base, succeeded by quartz sandstone and siltstone (Smith 1965). Elsewhere a basal clastic interval of varying thickness occurs, sometimes containing pelletal or pebble skeletal grainstone. The clastic to carbonate ratio increases as the formation is followed from north to south.

Three petroleum exploration wells and a Geological Survey of Queensland stratigraphic corehole have penetrated the Nora Formation (text-fig. 1) which, together with surface outcrop measurements, give some idea of the thickness and lithological variation within the formation in the Toko Syncline. Drilling in the Netting Fence Anticline in the northern part of the Toko Syncline (unpublished well completion report, Papuan Apinaipi Petroleum Co. Ltd., 1965), penetrated 114 m of Nora Formation which consisted of 41 m of sandstone, shale, and coquinite, overlain by 73 m of fine sandstone and shale. This total correlates well with a similar sequence, 119 m thick, in the Pulatera Hills in the central portion of the Toko Range, and the approximate 100 m measured in the type area. At the southern end of the Toomba Range, the Nora Formation is 250 m thick in AOD Ethabuka No. 1 (unpublished well completion report, Alliance Oil Development, Australia N.L. 1975) where it is reportedly composed mainly of shale with minor amounts of dolomitic sandstone and coquinite. Similarly, at the extreme southern end of the Toko Range, GSQ (Geological Survey of Queensland) Mount Whelan No. 2 stratigraphic hole penetrated 235 m of Nora Formation, again mainly composed of silty shale and sandstone with minor limestone (Green and Balfe 1980, p. 173).



TEXT-FIG. 1. Location and geographic distribution of the Nora Formation in central Australia.

Elsewhere, the Nora Formation is 70–100 m thick in the Tarlton Range (Smith 1965, 1972), where it conformably overlies sandy carbonates and dolomites ascribed to the Kelly Creek Formation, the Coolibah Formation not being recognized (Smith 1972, p. 128). The internal lithostratigraphy of the Nora Formation in the Tarlton Range is similar to that in the northern Toko Range. At the eastern end of the Dulcie Syncline, in the Huckitta district some 120 km further west, Smith (1963*b*) has recorded a predominantly dolomitic, coquinitic, ferruginized sequence (including oolitic ironstone) up to 125 m thick, and conformably overlying Tomahawk Beds of late Cambrian and early Ordovician age.

Webby (1978, 1981) has correlated the Nora Formation of the Georgina Basin with the Horn Valley Siltstone of the Amadeus Basin, and the Willara and Gap Creek Formations of the Canning Basin in Western Australia. On the basis of these correlations, Webby (1978, fig. 6*b*) has reconstructed a palaeogeography for late early Ordovician time wherein the Nora Formation is deposited under the influence of a warm equatorial current in a narrow, basically east–west orientated, Larapintine Sea. Within this seaway, Draper (1977) considers the Nora Formation to represent below wave base sediments, in part contemporaneous with sand bars (Carlo Sandstone on his fig. 2) and lagoon bay sediments (Mithaka Formation on his fig. 2), but there is no palaeontological evidence to confirm this relationship. As far as regional correlation of stratigraphic units within this seaway go, the conodonts of the Horn Valley Siltstone suggest a mid-Arenig age, within the *Oepikodus evae* and *Baltoniodus navis*/*B. triangularis* Biozones of the Baltic region, according to Cooper (1981). Based on this information, and as yet unpublished conodonts from the Georgina Basin, Cooper (*op. cit.*) concluded that the Horn Valley Siltstone is equivalent to the Coolibah and basal Nora Formations of Toko Syncline, thus supporting our contention (below) of a mid–late Arenig age for the Nora Formation. While this information does not alter the palaeogeographic picture, it may suggest a certain diachroneity of the stratigraphic units correlated by Webby.

		TOKO/TOOMBA RANGE		TARLTON RANGE	DULCIE RANGE
MESOZOIC (undiff – erentiated)	DEVONIAN	HOORAY SANDSTONE		TARLTON FORMATION	
		CRAVENS PEAK BEDS (sensu stricto) (late early-mid Devonian)		CRAVENS PEAK BEDS (exact age uncertain)	DULCIE SANDSTONE (early-late Devonian)
ORDOVICIAN	MIDDLE	ETHABUKA SANDSTONE	TOKO GROUP		
		MITHAKA FORMATION		MITHAKA FORMATION	
		CARLO SANDSTONE		CARLO SANDSTONE	
	EARLY	NORA FORMATION		NORA FORMATION	NORA FORMATION
		COOLIBAH FORMATION		COOLIBAH FORMATION	
		KELLY CREEK FORMATION		KELLY CREEK FORMATION	
LATE CAMB- RIAN		NINMAROO FORMATION		NINMAROO FORMATION/ TOMAHAWK BEDS	TOMAHAWK BEDS

20/A/16

TEXT-FIG. 2. Stratigraphic relationships of the Nora Formation to adjacent Formations in central Australia.

AGE OF THE NORA FORMATION

The Nora Formation is in places extremely fossiliferous and, collectively, a large biota has been recorded: bivalves, nautiloids, gastropods, rostroconchs, brachiopods, ostracodes, bryozoans, pelmatozoa, sponges, corals, conodonts, trilobites, ichnolites, and questionable foraminifera (see Shergold and Druce 1980, p. 163). Of these groups, some actinoceratoid nautiloids have been described by Beard (*in Hill et al.* 1969) and Wade (1977a, b), and these are considered to have an early middle Ordovician age. Similarly, the conodonts illustrated by Nieper (*in Hill et al.* 1969) are ascribed an early middle Ordovician age, by virtue mainly of the presence of *Histiodella*. This is disputed by Druce (*in Shergold and Druce* 1980, p. 163) who regards the Nora conodonts as indicating an age late in the early Ordovician (late Arenig), based on the presence of non-fibrous Scandinavian forms. The Nora Formation has also yielded ten species of bivalves which include an ambonychiid form, a family not known elsewhere earlier than the beginning of the middle Ordovician. Together with the other bivalve evidence, Pojeta and Gilbert-Tomlinson (1977, pp. 4–5) suggest an age near the early/middle Ordovician boundary. The rostroconch species *Technophorus* sp. and *Euchasma skwarkoi* described by Pojeta *et al.* (1977) are not age diagnostic. The orthoid and plectambonitid brachiopods, a variety of gastropods (?*Lophospira*, ?*Clathrospira*, ?*Helicotoma*, a bellerophonitid), a monoplacophoran, and the ichnolites, are yet to be described in detail, although some are illustrated by various authors *in Hill et al.* (1969).

The definition of lower and middle Ordovician in the preceding discussion is that customarily adopted by North American workers; the base of the middle Ordovician is taken at the base of the Whiterock Stage of the North American platform sequence at a horizon approximately equivalent to the base of the Llanvirn. Part of the apparent conflict between lower and middle Ordovician determinations in the Nora Formation may be a reflection of the correlation problems involved with the Whiterock Stage. Fortey (1980d) has suggested that the Whiterock is diachronous and often underlain by an interval in which shelly fossils are rare, or a disconformity, equivalent at the least to the upper part of the Arenig Series. Faunas of 'Whiterock aspect' (e.g. Wade 1977a) may appear within this interval if the appropriate facies is developed. To give one example, Hill *et al.* (1969, pl. O-IV, fig. 3) figure *Cacheoceras trifoldum* Flower, 1968 from the Nora Formation. Flower's original description cites the horizon as 'certainly within Zone K of Ross (1951)' (Flower 1968, p. 32). If the base of the Whiterock is taken as the base of the succeeding Zone L, as is usual, then this occurrence indicates lower, not middle, Ordovician. Correlation of Zone K with the late Arenig was suggested by Fortey (1980a); so the cephalopod and trilobite evidence below are not greatly at odds.

The trilobite fauna described here is mostly endemic to Australia. Of the endemic genera, *Fitzroyaspis*, *Gogoella*, and *Namibeetella* are all present in the Canning Basin in Arenig rocks (Legg 1976), but we have determined all our forms as new species so they cannot be used for precise correlation. *Presbynileus* cf. *utahensis* is compared with a species from zone J of Utah (Hintze 1953) which correlates with the middle part of the Arenig Series (Fortey 1976). Among the pelagic forms, *Carolinites genacinaca* occurs in the earliest part of the Nora Formation only, the upper part having *C.* cf. *ekphymosus*. *Carolinites* spp. with narrow fixed cheeks like the latter are not known outside Australia before the late Arenig (*Isograptus* Zone and equivalents), while *C. genacinaca* is widespread in mid-Arenig faunas over a great area (Fortey 1975). So, on the evidence of these species comparisons, the Nora Formation is assuredly Arenig and probably belongs within the middle and upper part of the Series (for informal definitions of lower, middle, and upper Arenig see Cooper and Fortey 1982). If this assessment is correct, it means that several of the trilobite genera in the Nora Formation are making their first appearances. *Hungioides* is elsewhere Llanvirn; *Prosopiscus* and *Phorocephala* have previously recorded ranges from Llanvirn to Caradoc; *Annamitella* is widely distributed in rocks of late Arenig and Llanvirn age. For correlation purposes we place more emphasis on the few, close species-level comparisons than on the generic composition as a whole.

Zonal subdivision

The Nora faunas divide broadly into two; since the facies is similar throughout we can recognize two assemblage zones, with the bulk of the Formation lying in the upper Zone. The readiest zonal guides are the extraordinary endemic asaphids of the genus *Norasaphus* which are also common in most localities. The lower Zone of *N. (N.) skalis* is dominated by the eponymous species but also includes: *Lycophron* sp. A., *C. genaciuaca*, *Annamitella strigifrons*, *Phorocephala* cf. *P. genalata* Lu. The upper Zone of *N. (Norasaphites) monroae* includes also: *N. (N.) vesiculosus* (common), *Lycophron rex*, *A. glabra*, *Presbynileus* cf. *P. utahensis* (Hintze), *C.* cf. *C. ekphymosus* Fortey, *Naubeetella embolion*, *Hungioides acutinasus*, *G. brevis*, and *F. irritans*. *Prosopiscus* spp. span both zones (text-fig. 3). The few trilobites in common with the faunas of the Canning Basin indicate a broad correlation with Fauna 3 of Legg (1978). Because trilobites become rare at the top of the Nora Formation it is not possible to pick up overlap between the Nora faunas and those of the overlying Carlo Sandstone, although sedimentation appears to have been continuous.

PRESERVATION OF THE TRILOBITES

Most of the trilobites are preserved as moulds in fine sandstones. All are fragmentary and some of the larger pieces are broken. Some beds are full of fine trilobitic hash. The detail preserved on external moulds varies from locality to locality, but at its best the preservation is good enough to show sculptural details. All specimens are in full relief. A few beds in the lower part of the Nora Formation are carbonate-rich, and in these the trilobites are preserved with their exoskeleton intact. The fragmentary nature of the fossils makes association of the different parts especially difficult, and we have stated the reasons for making particular associations where these are not obvious. It seems there has been post-mortem sorting of the trilobites, and it is not possible to identify 'communities' in the fauna. Yet the endemic character of most of the fauna indicates that the trilobites all lived in an inshore, cratonic environment.

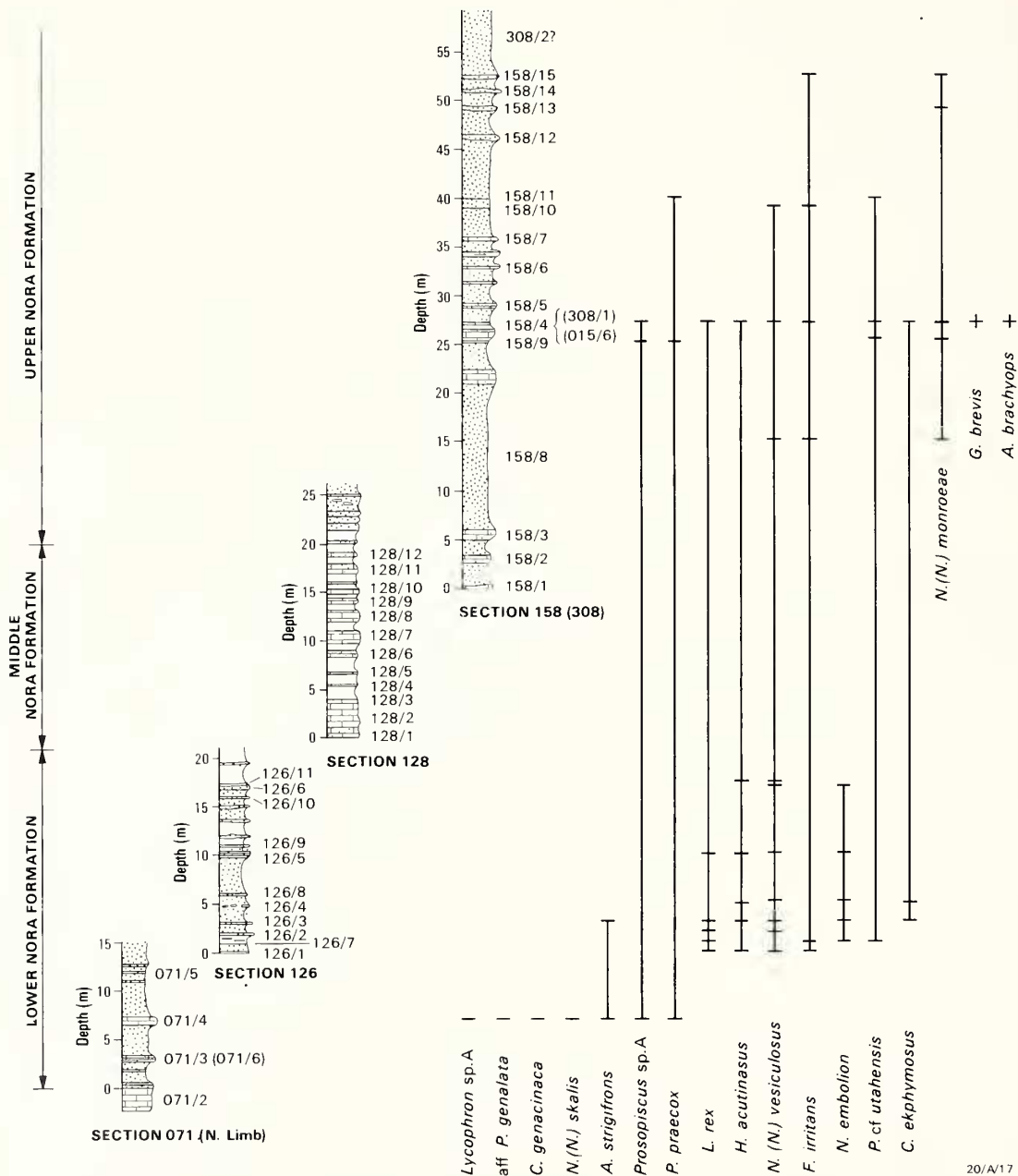
BIOGEOGRAPHIC ASSESSMENT OF THE NORA FORMATION FAUNA

Shallow-water cratonic faunas like that from the Nora Formation are the most sensitive indicators of provincial affinities (Cocks and Fortey 1982), being specifically adapted to ambient temperature and substrate conditions. It is appropriate to consider what the Nora trilobite faunas tell us about the early Ordovician palaeogeography of Australia. Sedimentology of earlier Ordovician formations (Radke 1981) indicates limestone deposition under tropical conditions; the occurrence in Australia of early Ordovician cephalopods (Gilbert-Tomlinson, *in* Hill *et al.* 1969), molluscs and conodonts (Druce and Jones 1971) known elsewhere from areas lying near the palaeoequator, as well as typical 'Pacific' province graptolites in Victoria, all leave no reason to doubt that Australia straddled low latitudes in the earlier part of the Ordovician. Larval dispersal doubtless varied considerably from one group to another, and the trilobites tend towards endemism more than, say, conodonts. This means that the trilobites are a better guide to former continent separation than many other groups, although concomitantly less useful in inter-regional correlation. Comparisons are considered at generic and specific level.

In the first place there are a few elements in the Nora trilobite fauna which are familiar from North America at a considerable distance around the equatorial great circle. These are *Caroliinites* spp., a species intermediate between *Goniophrys* and *Phorocephala* (= *Carrickia*), and a *Presbynileus* species close to, if not identical with, one from Utah and Nevada. The first two named belong to the pelagic family Telephinidae; their independence from facies type and continent distribution, and their circum-equatorial distribution, has been familiar for some time (Fortey 1975). The last named is so far unrecorded outside North America. These aside, there is little in common between faunas from North America, or north-eastern Siberia, and that from the Nora Formation, and when apparently similar forms appear (e.g. *Lycophron* gen. nov. compared with *Isotelus*) this is because of convergence rather than phylogenetic continuity.

The most common trilobites in the Nora Formation, comprising about 85 per cent of the benthic

elements, are a group of curious endemic asaphids (*Lycophron*, *Fitzroyaspis*, *Norasaphus*), especially the unique tuberculate genus *Norasaphus* which frequently covers entire bedding planes. Two other genera, *Gogoella* and *Nambeetella*, were described by Legg (1976) from the Canning Basin, north-western Australia (but for taxonomic problems see systematic section). Well over half the benthic forms are unknown outside Australia and include the dominant elements in the fauna.



TEXT-FIG. 3. Composite stratigraphic section through the Nora Formation with ranges of trilobites.

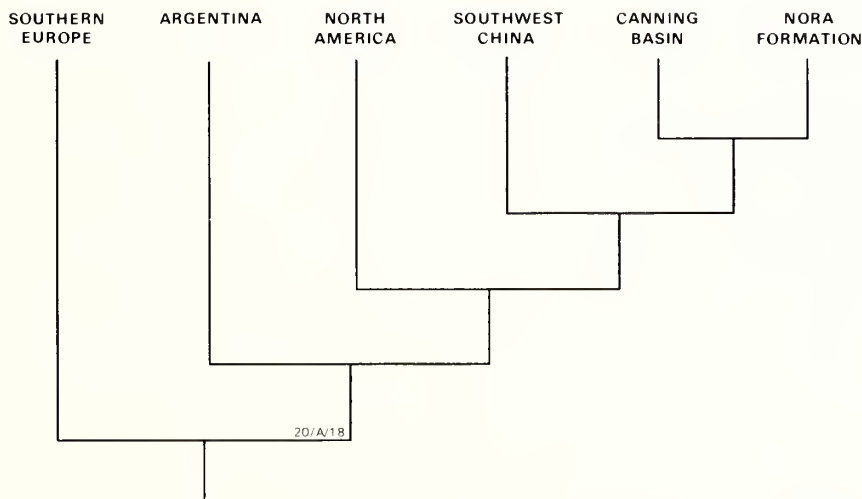
There remain a few genera which are 'Gondwanan' in distribution, notably *Hungioides* and *Prosopiscus*. Both occur in southern China. *Hungioides* has a wide distribution through South America (= *Argentinops* Přibyl and Vaněk 1980) to Bohemia and Thuringia. *Prosopiscus* occurs also in the Himalaya (Salter 1865). Finally, the genus *Annamitella* is very widely distributed through China, Kazakhstan, Vietnam, and with various occurrences off volcanic islands in Maine, Newfoundland, and Anglesey, Wales. Although such a spread might suggest planktonic habits like the Telephinidae there is nothing in the morphology of *Annamitella* to suggest that this was the case.

Only one explanation seems to us to explain the different elements combined in the Nora trilobite faunas. An equatorial position explains the pelagic elements, the dispersal of which is not inhibited by distance. Yet the dominance of peculiar endemics implies that platformal Australia was separated from other cratonic areas near the Ordovician palaeoequator sufficiently to induce speciation among available families—especially Asaphidae. A few forms (*Annamitella*, *Presbrynileus*) were more widely distributed, probably because of efficient larval dispersal. Finally, the presence of otherwise Gondwanan elements suggests that Australia may have been attached to, or at least close to, the rest of Ordovician Gondwanaland (as in the reconstruction of Scotese *et al.* 1979), sufficient for the penetration of a few more eurytopic genera. Text-fig. 4 summarizes the relationships of the Nora Formation trilobites to those of other areas.

It is interesting to note that the fauna from the Canning Basin described by Legg (1976) is the closest to that from the Nora Formation (six genera in common), but it also includes a number of very widely distributed benthic genera such as *Triarthrus*, *Ampyx*, *Shumardia*, and *Ogygiocaris*. Both the lithologies and associated graptolites and conodonts (North Atlantic community type) indicate that deeper water, peripheral-cratonic facies are represented in this area. These include biofacies deep enough not to be restricted geographically in the same way as the on-craton faunas of Queensland and the Northern Territory.

SYSTEMATIC DESCRIPTIONS

Terminology follows that of the *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1* (Harrington, Moore, and Stubblefield, in Moore 1959), with the addition of certain terms from Őpik (1967) and Fortey (1975). Glabella is usually understood to include the occipital ring. Systematic order is by family as they appear in the Treatise.



TEXT-FIG. 4. Diagram to show relative resemblances at generic level of the trilobite faunas from the Nora Formation to those of other areas. The scale ranges from six genera in common in the Canning Basin to one only in southern Europe.

Family LEIOSTEGIIDAE Bradley, 1925

Discussion. We extend the concept of the Leiestegiidae to include a number of Ordovician genera which have hitherto been referred to other families. In particular, we regard *Annamitella* (and its three possible synonyms *Bathyriscops*, *Monella*, and *Proetiella*) as belonging to a late radiation of the leiesteguids in which the dorsal furrows are fully expressed. Species of this type have been regarded as bathyurids (Whittington 1963). Recent revision of Canadian bathyurid genera (Fortey 1979) shows that any resemblances to that family are misleading, and that *Annamitella* and related forms are not closely comparable to either Bathyrinae or Bathyrellinae. In particular the long, anteriorly truncate glabella (concave-sided in some species) and the straight, inward- and backward-directed IP glabellar furrow are not bathyurid features; in the latter the IP furrows, when developed, are broadly arched or hooked backwards. The pygidium is possibly most similar to that of *Bathyrina* among bathyurids, but again the resemblance is misleading as there are twice as many axial segments in most species of *Annamitella*, and the broad, convex pleural fields surrounded by a narrow, 'rolled' border are leiestegiid features. It also seems likely that *Agerina* Tjernvik, 1956, which shares glabellar characters with *Annamitella*, should be removed from the Bathyridae. The pygidium in this genus is much smaller than in *Annamitella*, however. *Leiestegium* itself and its close relative *Lloydia* are highly effaced genera, but since effacement is of all trilobite characters the one most susceptible to polyphyletic derivation, it is apparent that subdued furrows cannot be used in the definition of the superfamily, as in the *Treatise* (Lockman-Balk in Moore 1959, p. 313). Of *Lloydia* species with an elongate glabella like that of *Annamitella* we may cite *L. oblonga* (Billings) from the Lévis Conglomerate. There is also a tendency in *Lloydia* for the border to become reclined against the glabella, a process carried to completion in *Annamitella*. Note also that there are strong apodemal pits at the anterolateral corners of the glabella in *L. bituberculata* (Billings), pits which occur in exaggerated form in the homologous site in *Annamitella*. It is also possible to see muscle insertion areas on the glabella of *L. spp.*, comparable in form (though more anteriorly placed) to those in *Annamitella*.

Transitional forms between conventional Leiestegiidae and *Annamitella* occur in Tremadoc rocks. In particular the genus *Szechuanella* Lu, 1959 (type species *S. szechuanensis*—see Lu 1975, p. 3, figs. 3–9) has a pygidium almost indistinguishable from that of *Annamitella*, while the cranium, although relatively effaced, clearly shows the backward-directed IP glabellar furrow, and the border is tipped back against the front of the glabella. Co-apertive structures like those described below in *Annamitella* have been described on *Pagodia* (*Wittekindtia*) *variabilis* by Wolfart (1970, pl. 8, fig. 5b). Lu (1975, p. 458) also erected a new family Eucalymenidae for some Arenig–Llanvirn trilobites from central China. Lu included two genera in the family: *Eucalymene* Lu, 1975 (itself a probable synonym of *Pseudocalymene* Pillet, 1973) and *Bathyriscops* Lisogor, in Keller and Lisogor, 1954. As discussed below, the latter is a subjective synonym of *Annamitella*. The former resembles *Szechuanella* and differs from *Annamitella* in its relatively small palpebral lobes being somewhat removed from the glabella, and in the characters of the cranial border. *Eucalymene* has strong glabellar furrows of *Annamitella* type; its pygidium has interpleural furrows, and the pygidial border is almost obsolete. These characters are scarcely of familial significance. Hence, we regard the Eucalymenidae as synonymous with the Leiestegiidae.

Once the Leiestegiidae is extended to include forms *en grande tenue*, we can speculate on the inclusion of other candidates within at least the same superfamily. When three glabellar furrows are developed on *Annamitella*, they have a distinctive form, with 1P steeply backward-inclined, 2P only gently so, and 3P anteriorly directed close to 2P. The same kind of furrow arrangement is seen on the diminutive earliest Canadian genus *Missisquoia* (particularly the type species *M. typa*, e.g. Stitt 1971, pl. 8, fig. 2). The systematic position of *Missisquoia* has long been problematic; the family Missisquoidae Hupé, 1953, is generally regarded as of uncertain ordinal affinities, although Shergold (1975, 1980, 1982) has consistently referred the family to the Leiestegiacea. We propose that *Missisquoia* is a neotenous derivative from a leiestegiacean. Additional features suggestive of a neotenous origin include especially the pygidium, in which the numerous segments are arranged as

if 'ready for release', and the extremely long, narrow glabella (which is like smaller *Annamitella*). Curiously, we have never seen leiostegiids in the same beds as *Missisquoia*, and so it does not seem probable that the small trilobite is simply a growth stage of a larger, more conventional leiostegiid.

Genus *Annamitella* Mansuy, 1920

Type species. Annamitella asiatica by original designation.

Revised diagnosis. Leiostegiid genus with dorsal furrows strongly expressed. Glabella long, subparallel-sided to slightly tapering forwards, with a tendency towards a slight expansion of the frontal lobe in some species. Two or three pairs of glabellar furrows, 1P straight and strongly backward-directed, 2P more transverse. Frontal border incorporated into glabella medially. Eyes large, close to glabella; width of preocular cheeks correspondingly reduced. Genal spines long to reduced. Pygidium strongly furrowed, four to nine axial rings, five or six pleural ribs. Axis extends to near posterior margin. Pygidial border variable, usually narrow and convex, but may be almost absent, to moderately broad and flattened.

Discussion. Dean (1973) and Whittington (1963) have noted that *Bathyriscops* Lisogor, in Keller and Lisogor 1954, *Proetiella* Harrington and Leanza, 1957, and *Monella* Bates, 1968 could all prove to be synonyms of *Annamitella*. Our well-preserved material of *Annamitella* enables some clarification of the problems involved.

The material of the type species *A. asiatica* Mansuy (1920, pl. 2, figs. 7a-k) is not entirely satisfactory, being somewhat distorted internal moulds. Nevertheless, they do show the long glabella, two pairs of glabellar furrows, and, most important, what Mansuy interpreted as a third pair of glabellar furrows—in fact the trace on the internal mould of the lateral edge of the anterior border (cf. Pl. 38, fig. 4). The pygidium is like that of our Australian species, but with one less pleural rib posteriorly, a narrower border, and one or two less axial rings. But these differences are scarcely of generic standing, and we regard our assignment of the species from the Nora Formation as well-founded. The type species of the other genera named above are also poorly preserved. *Bathyriscops*, type species *B. granulatus* (Weber 1948, pl. 1, figs. 22–24; also Keller and Lisogor 1954, pl. 1, figs. 1–7; Chugaeva 1958, pl. 1, figs. 1–3) from the Llandeilo of Kazakhstan, is also apparently known from exfoliated material but, except for deeper glabellar furrows (and in some of the figured specimens a greater median contraction of the glabella), the resemblance to our species is overwhelming; *Bathyriscops* is accordingly regarded as a subjective synonym of *Annamitella*. *Proetiella* from the Llanvirn of Argentina is also closely similar in all major features, but one specimen of a cranidium of the type species (*P. tellecheai*, see Harrington and Leanza 1957, fig. 59, 3) shows what is probably a 3P glabellar furrow immediately in front of 2P. The type species of *Monella* (*M. perplexa* Bates, 1968, from the Arenig rocks of Anglesey) is very badly preserved but also shows evidence of the 3P glabellar furrow (e.g. Bates 1968, pl. 11, fig. 18), so there may be a case for regarding the presence of the 3P furrow as a generic discriminant. Unlike the type species of the other genera, *M. perplexa* has a broad and probably flattened pygidial border. The Australian species have a broader anterior cranial border (vertically) than any of the species discussed so far, also well-developed co-apertive devices; no other species have been described fully enough to be sure whether structures similar to the latter were present or not. In any case we do not regard the presence of such structures as of generic significance because they are found in several leiostegiids.

In summary, we incline to the view that *Annamitella* is the senior synonym of *Bathyriscops*, *Proetiella*, and *Monella*. Further information on *P. tellecheai* may possibly allow for the discrimination of a second genus (of which *Monella* will be a junior synonym), but the presence of a 3P glabellar furrow alone seems inadequate grounds for so doing at the moment. Taking the broad view of *Annamitella* advocated here the following described species may be assigned to the genus: *A. asiatica* Mansuy, 1920; *B. granulatus* (Weber, 1948); *P. tellecheai* (Rusconi, 1951); *B. kantsingensis* Chang and Fan, 1960; *A.? borealis* Whittington, 1963; *M. perplexa* Bates, 1968; *A.? insulana* Dean,

1973; and *A? guizhouensis* Yin, 1978. North American and European occurrences seem to be confined to Ordovician volcanic islands, but the Asiatic and southern hemisphere occurrences are apparently in normal platform facies.

Annamitella strigifrons sp. nov.

Plate 38; text-fig. 5

Diagnosis. *Annamitella* species with granulate surface sculpture. Anterior border, incorporated into glabella, forming a wide anterior wall on cranidium, carrying raised lines. Palpebral lobes very long, anterior limit at or in front of 2P glabellar furrow. Pygidium with seven or eight axial rings, and distinct, narrow convex border. Genal spines reduced to stub on large free cheeks.

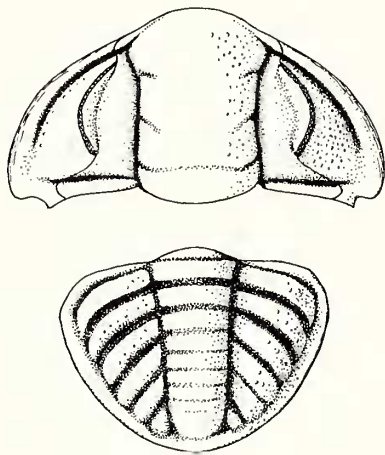
Derivation of name. Latin *strigifrons*, 'ridged-front'.

Holotype. Largely exfoliated cranidium, CPC 22642, from loc 071/4.

Other material. Cranidia, CPC 22643–22645, 22775, 22776; librigenae, CPC 22646–22648, 22777; pygidia, CPC 22649–22652, 22778–22782.

Occurrence. Lower part of Nora Formation, locs. 071/4, 126/3.

Description. Most of the material is stripped of exoskeleton, but enough remains to describe the dorsal surface of this species. The cuticle is very thick and the internal mould retains little trace of the surface details. Since most other species of *Annamitella* have been described from exfoliated material it is evident that many of the salient details are not known from these. All furrows internally are deeper and wider.



TEXT-FIG. 5. *Annamitella strigifrons* sp. nov. Reconstruction of cephalon and pygidium, about $\times 2$.

EXPLANATION OF PLATE 38

Figs. 1–15. *Annamitella strigifrons* sp. nov. Loc. 071/4 (1–13) and loc. 126/3 (14, 15). 1, 2, CPC 22643, cranidium retaining cuticle but damaged posteriorly; dorsal (1) and anterior (2) views to show incorporation of border into frontal lobe of glabella, $\times 6$. 3, 5, CPC 22642, holotype, well-preserved, but largely exfoliated cranidium in dorsal (3) and anterior (5) views, $\times 6$. 4, CPC 22644, typically preserved internal mould of cranidium, $\times 5$. 6, CPC 22646, testate free cheek with ridges as well as tubercles, tilted forwards to show posterior margin, $\times 6$. 7, CPC 22645, small cranidium, internal mould, $\times 7$. 8, CPC 22647, small free cheek, internal mould showing genal spine, $\times 7$. 9, 10, CPC 22648, well-preserved free cheek in dorsal (9) and anterior (10) views, the latter showing notch in border, $\times 7$. 11, CPC 22649, lateral view of internal mould of pygidium, $\times 6$. 12, CPC 22650, small pygidium, $\times 8$. 13, CPC 22651, pygidium largely retaining cuticle, $\times 6$. 14, 15, CPC 22652, typical internal mould preservation of pygidium; dorsal view (14), and latex cast (15) from second specimen on same rock piece photographed from anterior end to show doublure and pair of prominent prongs proving relationship with pagodiids, $\times 6$.



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Cranidium of sagittal length about three-quarters maximum width across posterior margin. Glabella of relatively low transverse convexity, not projecting above level of intraocular cheeks, sloping downwards steeply over anterior half, width at mid-length a little over half maximum sagittal length (dorsal view). Glabella tapers forwards gently, to minimum width at 2P glabellar furrows, with frontal lobe expanding in width more rapidly towards anterolateral corners; front margin broadly rounded about mid-line. Deep occipital furrow, deepest laterally and gently forward-arched medially, so that the occipital ring correspondingly widens medially. Two pairs of glabellar furrows, both deep, short, and straight to very gently curved; 1P opposite mid-length of palpebral lobes, steeply inward-backward inclined, 2P about halfway between 1P and anterior border (exsag.), transverse to slightly backward inclined. No trace of 3P furrow on larger crania, but a small cranium (Pl. 38, fig. 7) shows a faint pair of dimples which may be the vestiges of 3P. The small cranium also has a narrower glabella with less taper posteriorly. Axial furrows are hugely deepened at the anterolateral corners of the glabella to form a pair of stout, ventrally-directed apodemes which presumably articulated with the wings of the hypostoma. The anterior cranial border is defined immediately in front of these pits, where it is narrow (exsag.) and ridge-like. Adaxially the border merges with the front of the glabella, and the furrow defining it becomes obsolete quite rapidly. The course of the border is, however, revealed by the ridges that cover its outward-facing surface (Pl. 38, fig. 2); one specimen shows a slight median dip in the height of the border.

Preocular cheeks steeply downward sloping, narrow (tr.) and convex. Gently arcuate palpebral lobe extremely large, forward end closest to glabella, opposite or slightly in advance of outer end of glabellar furrow 2P, posterior end at occipital furrow. Palpebral furrow deep, broadly outward-bowed, outlining a convex, relatively narrow palpebral rim. Cheeks inside palpebral lobes are somewhat inflated. Postocular cheek triangular, width (tr.) about two-thirds that of occipital ring, with deep transverse border furrow, and narrow, convex posterior border which widens laterally. Sutures diverge at a high angle behind palpebral lobes; anterior divergence slight, subparallel with anterior expansion of frontal glabellar lobe; they then appear to converge across downward slope of border before running across edge of border to meet at mid-line. Dean (1973, pl. 7, fig. 8) seems to have incorrectly interpreted the steep border as a rostral plate.

Surface sculpture on glabella and occipital ring of dense and posteriorly somewhat flat-topped tubercles, stopping abruptly at fine elevated ridges on vertical part of border. Free cheek with outline in dorsal view almost a quarter circle, genal fields broadly convex. Genal spine reduced to small stub, but still present on small cheeks (Pl. 38, fig. 8). Lateral border furrow exceedingly deep and narrow anteriorly, but shallowing abruptly and dying out near genal angle. Major part of lateral border a steep, outward-facing 'wall' continuous with that on cranium, excavated by a deep notch at about mid-length. This notch received a prong on the pygidial doublure during enrolment, a co-aptative device for this species. Exterior to the notch the border is less steep. Posterior border carries a broad, backward-directed projection of about the same dimensions as the genal spine remnant; presumably this was connected with the anterolateral articulation of the first thoracic segment. Eyes not preserved; beneath the eye there is a deep, smooth groove. Sculpture on genal fields tuberculate like glabella. One specimen has some of the tubercles carried on low ridges (Pl. 38, fig. 6); we incline to the view that this is an intraspecific variant, particularly as there is a tendency on the other cuticulate specimen for the tubercles to form lines, and the cheeks agree in all other respects.

Pygidium with maximum width near anterior margin, 1.3–1.4 times sagittal length including half-ring. Width of axis at anterior margin equal to, or slightly exceeding, that of adjacent pleural field plus border. Axis tapers initially very gently, becoming parallel-sided at fourth or fifth axial ring. Up to eight axial rings are present, which become only slightly narrower (sag.) backwards, of which the first four or five are clearly defined, the seventh and particularly the eighth (which is not discernible on some internal moulds) poorly so. Small rounded terminal piece. Axis extends to border to which it slopes down almost vertically. Pleural fields broadly convex (tr.). Pleural ribs flat-topped on exterior surface, separated by deep furrows of about half their width; on internal moulds the dimensions are reversed, with furrows exceeding width of more rounded ribs. Six pairs of such ribs, the last developed as triangular nodes adjacent to the terminal piece of axis. Border of same width as axial rings, continuous around posterior perimeter, gently convex. Steeply downsloping triangular facets less than half width of anterior margin. Pygidial doublure (Pl. 38, fig. 15) steeply reflexed inside border and narrowing a little medially. Anterolateral edges carry a pair of prominent, ventrally projecting prongs, visible as pits in the external mould, which obviously served to engage with the notches in the cephalic border during enrolment. Exterior to the prong there is a slight groove which probably received the lateral edge of the median part of cephalic border. Small pygidium (Pl. 38, fig. 13) is slightly longer, and shows only seven axial rings, with a longer terminal piece on the axis.

Discussion. No other species of *Annamitella* is preserved as well as *A. strigifrons*, and comparisons are generally difficult, although Dean (1973) showed that the exterior surface of *A. insulana* (Arenig-

Llanvirn, Newfoundland) was tuberculate, and with a comparable cranidial border ('rostral plate' of Dean 1973, pl. 7, fig. 8). *A. insulana* is otherwise difficult to compare, being greatly distorted. However, the palpebral lobe is assuredly shorter, and there is a genal spine in the adult of this species. The type species (Mansuy 1920, pl. 2, figs. 7a-k) has a longer frontal glabellar lobe (more like our immature specimen), the pygidial border appears to be much reduced, and there are apparently no more than six axial rings. *A. borealis* Whittington, 1963 apparently lacks tubercles externally, has the 2P glabellar furrow effaced, a narrower cephalic border, genal spines, and fewer pygidial segments defined. *A. guizhouensis* Yin, 1978 also has large eyes, but has a distinct 3P glabellar furrow, and the pygidium has only four pairs of ribs. *A. kantsingensis* (Chang and Fan 1960, pl. 5, figs. 9-12) includes granulate cranidia, but with the glabella expanding uniformly forwards, the one pygidium (ibid., fig. 11) with a much broader, flattened border than in *A. strigifrons*. The latter character also distinguishes *A. monensis* Bates, 1968 which additionally has a much narrower cranidial border, defined faintly across the mid-part of the glabella. The pygidial proportions of *A. tellecheai* (Harrington and Leanza, 1957) are closely similar to the Australian species; cranidial differences include the probable presence of a 3P glabellar furrow, a (?) narrow cranidial border (ibid., fig. 59, 7), and smaller palpebral lobes that fall short of the 2P glabellar furrow. The closest species to *A. strigifrons* is *A. granulata* from the Karakansk Formation of Kazakhstan (Keller and Lisogor 1954, pl. 1, figs. 1-7; Chugaeva 1958, pl. 1, figs. 1-3). This species has eyes as large as *A. strigifrons*, and seems to lack genal spines. Posterior forward taper of the glabella (adjacent to the IP lobe) is very strong on the Kazakhstan species, however, and there are only four fully developed pleural ribs on the pygidium, the fifth pair being represented by triangular remnants, as is the sixth pair on *A. strigifrons*.

The very wide dispersal of a whole suite of closely similar species may lead one to wonder whether this genus had pelagic habits. Curiously, *Annamitella* does not seem to have penetrated into the platform carbonates of either North America or north-east Siberia. It seems to be associated particularly with clastic facies, as it is in Australia, and if this is the case then it must have spent much of its life feeding near the bottom; but its dispersal remains wider than that of any other genus in the Nora Formation apart from the truly pelagic *Carolinites*.

Annamitella brachyops sp. nov.

Plate 45, figs. 15-17

Diagnosis. *Annamitella* with short (exsag.) and highly curved palpebral lobes; glabella parallel-sided and broadly rounded in front; IP glabella furrows gently curved. Sculpture of granules.

Derivation of name. Greek *brachyops*, 'short-eyed'.

Holotype. Cranidium, CPC 22772, from loc. 308/1.

Material. Cranidia, CPC 22773, 22783-22785; pygidia, CPC 22774, 22786-22788; small librigena, CPC 22789.

Occurrence. Upper part of Nora Formation, locs. 158/4, 308/1.

Discussion. This second species of *Annamitella* differs in several features from *A. strigifrons*: (1) the glabella is parallel-sided, rather than expanding at the frontal glabellar lobe which has a nearly semicircular outline in *A. brachyops*; (2) glabellar furrows, especially IP, are more transverse and gently curved in *A. brachyops*; (3) palpebral lobes are less than one-third (exsag.) length of whole cranidium in dorsal view, compared with one-half or more in *A. strigifrons*; (4) surface sculpture (but only seen on one external) apparently of rather discrete, fine granules. The palpebral lobes are nearly semicircular in *A. brachyops*. This difference makes the cranidium of *A. brachyops* relatively wide compared with that of *A. strigifrons*, width across palpebral lobes 1.4 to 1.5 times sagittal length, compared with 1.1 to 1.3 times in the latter. Pygidia of the two species are closely similar; posterior border on *A. brachyops* may be slightly wider laterally, and only five pleural ribs are clearly developed.

Of the species of *Annamitella* listed above only two have short palpebral lobes like *A. brachyops*:

these are *A. (Proetiella) tellecheai* Harrington and Leanza, 1957, and the material of *A. ('Bathyuriscops') granulata* illustrated by Weber (1948) and Chugaeva (1958). The type material in Weber (1948) of the latter has a long, narrow glabella with a strongly curved front margin, and the 1P glabellar furrow is certainly more oblique. The cranidium illustrated by Chugaeva (1958) from the Kopalín Formation in Kazakhstan, of late Arenig to Llanvirn age (Fortey 1975, p. 31), is extremely close to the Australian specimens, particularly with regard to the curved palpebral lobe symmetrically disposed about 1P, and may be conspecific. The Argentine species *A. macrophthalma* is also similar, and apparently granulate (Harrington and Leanza 1957, fig. 59, 7 bottom right), and really differs only in the distinctly truncate forward margin of the glabella, and the straight course of the 1P glabellar furrow.

Family ASAPHIDAE Burmeister, 1843
Subfamily ASAPHINAE Burmeister, 1843
Genus *Norasaphus* gen. nov.

Diagnosis. Asaphine trilobites with tuberculate or smooth dorsal surfaces. 1P glabellar furrows excavated as deep pits, or uniting across glabella to cut off basal glabellar lobe. Frontal glabellar lobe may become greatly inflated. Cephalic borders narrow but distinct. Long and narrow genal spines. Eyes small, far back. Cephalic doublure broad under cheeks, greatly narrowing medially, with very deep lateral marginal vincular furrow. Hypostoma with U-shaped notch, and maculae. Pygidium relatively small, with or without narrow border, with two to five axial rings defined. Pygidial pleural (and in some species interpleural) furrows exceptionally deeply incised.

Derivation of name. Combination of Nora (Formation) with *Asaphus*, to which genus the new one is related.

Discussion. This new genus includes the most extraordinary trilobites of the Nora Formation. Looking at the most advanced species (Pl. 40, fig. 1) it is difficult to imagine that such a *Phacops*-like trilobite could be an asaphid at all. In particular, dorsal tuberculation is otherwise unknown (and unlikely) in other asaphids, and its absence was used by Jaanusson (*in* Moore 1959, p. 334) as one of the defining characters of the family. However, we are certain that we have good grounds for assigning the closely related set of species from the Nora Formation to the Asaphidae. The stratigraphically earliest species, *N. (N.) skalis*, is also the most primitive, and, if we are able to ignore the dorsal tuberculation, is in most respects a typical asaphine, with its deep 1P apodemal furrows, well-defined occipital ring, and immediately pre-occipital glabellar tubercle. It may be compared with a genus like *Basiliella* Kobayashi, for example. The hypostoma is conventionally asaphine, as is the lateral vincular furrow on the free cheek. Subsequent evolution of the *Norasaphus* group produces exaggeration of the aberrant features. The 1P glabellar furrows become united across the glabella, producing a transverse furrow which chops off a basal median glabellar lobe. The posterior lobes adjacent to the glabella are discretely defined to become baculae. These advanced characters are the basis of the subgenus *Norasaphus* (*Norasaphites*).

Within *Norasaphus* (*Norasaphites*) one species (*N. monroeae*) loses cephalic tuberculation, acquires stalked eyes, and a tendency towards posterior effacement, while *N. (Norasaphites) vesiculosus* takes the peculiarities of *N. (Norasaphus) skalis* further, with very dense tuberculation and exceptional inflation of the frontal glabellar lobe, which in many specimens overhangs the anterior border, and highly incised furrows in all parts. This species is furthest removed from conventional asaphids, and yet we presume that all these profound anatomical modifications took place within the span of deposition of the Nora Formation, only a part of the Arenig Series (say about 5 million years). It is an indication of the flexibility of the external skeletal structure of the trilobites that such modifications can occur even in a generally conservative group like the Asaphidae when circumstances permit, and shows that caution is necessary to determine familial affinities in the face of homeomorphic resemblance.

We considered the possibility that the new forms merited subfamilial status. Since *N. (N.) skalis* is clearly an asaphine (*sensu* Fortey 1980a), and the new species taken together are more closely related

to other Asaphinae than to Niobinae or Isotelinae, in a phylogenetic classification they are to be included in the first-named subfamily, of which they are an extraordinary and probably short-lived branch.

What circumstances may be invoked to explain their unique modifications? Most inshore asaphids are the most highly effaced of the group, and their cuticle is not exceptionally thick (see, for example, *Isoteloides* in Fortey 1979). By contrast *Norasaphus* has a very thick cuticle (Pl. 39, fig. 1), but occurs with isotelines which are not unusual in this regard. In other shallow-water faunas of about the same age, for example the St. George (Catoche Formation) fauna of western Newfoundland, smooth isotelines occur with other trilobites with tumid glabellar frontal lobes, elevated eyes far back, thick cuticles, and strong tuberculate sculpture. In the St. George, the closest trilobite is *Petigurus* (redescribed by Fortey 1979), an anomalous bathyurid. *Petigurus* also has a pygidium with strong interpleural furrows, and a narrow border, superficially like that of *Norasaphus*. It is unlikely to be coincidence that both *Norasaphus* and *Petigurus* are convergent with *Phacops*, which was also adapted to carbonate facies of epeiric seas, in the Devonian. Phacopid convergence with *Norasaphus* extends even to pygidial details: the pygidium of *N. monrocae* is strikingly like that of *Eophacops*. We term this repeated morphological type the *phacomorph* design. Tubercles may have been partly concerned with strengthening the cuticle, but those of some of the phacopids have sophisticated internal structures ('pseudo-tubercles' of Miller 1976) which might argue for a more specific function. Eldredge (1971) has suggested that phacopids 'relied more heavily on labral secretion than appendage manipulation for ingestion' of food, which he associated with an oesophageal expansion housed beneath the inflated frontal glabellar lobe, like that so conspicuous on *N. (Norasaphites) vesiculosus*. The basal transglabellar furrow in phacopids and *Norasaphus (Norasaphites)* was presumably connected with the insertion of muscles for a powerful posterior appendage pair.

Whatever the functional explanation of phacomorph design, it was obviously one which could arise from different phylogenetic sources at different times, and was associated with inshore, or at least shallow-water carbonate habitats. In the case of midcontinent faunas, and both the St. George in Newfoundland and the Nora Formation in central Australia are typical examples, there seem to have been a limited number of potential stocks from which phacomorphs could be derived. We assume that the opportunity to occupy the phacomorph niche (or niches) was taken by the asaphids in Australia and the bathyurids in Newfoundland; in both cases their tenure of the niche was short-lived. The morphological distance travelled in a comparatively short time was considerable in both cases, which may relate to theories that the rates of evolution of inshore trilobites in warm climates were relatively rapid (Eldredge 1974; Fortey 1980b).

Subgenus *Norasaphus* subgen. nov.

Type species. N. (N.) skalis sp. nov.

Diagnosis. Subgenus of *Norasaphus* with tuberculate sculpture: glabellar furrows of normal asaphine type. Narrow pygidial border.

Norasaphus (Norasaphus) skalis sp. nov.

Plate 39; text-fig. 6

Diagnosis. *Norasaphus (Norasaphus)* is monotypic; diagnosis follows that of subgenus.

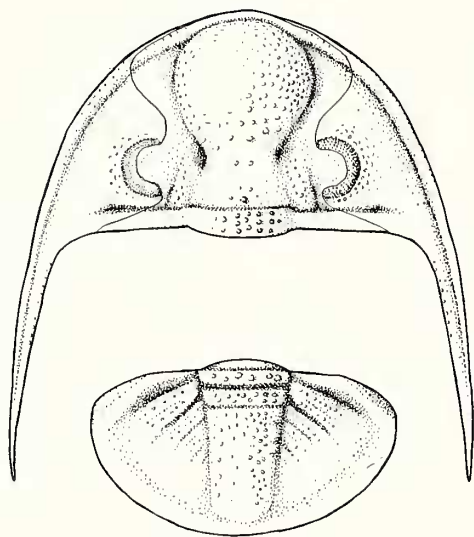
Derivation of name. Greek *skalis*, a hoe or mattock, referring to the shape of the anterior border.

Holotype. Cranidium, CPC 22653, from red limestones near base of Nora Formation, loc. 071/4.

Other material. Cranidia, CPC 22654–22660, 22790–22793; librigenae, CPC 22664, 22665, 22801, 22802; hypostomata, CPC 22666, 22667, 22803; pygidia, CPC 22661–22663, 22794–22800.

Occurrence. Numerous in lower Nora Formation at locs. 071/4, 127/2, 127/4, 127/12, 127/15.

Description. This species is known from well-preserved material in limestone, preserving details of the external cuticular surface. Cranidia have maximum width at posterior margin, only slightly greater than width across palpebral lobes, and about one and a half times maximum glabellar width at frontal lobe. Sagittal cranidial length about equal to maximum width. Glabella with maximum convexity across frontal lobe, minimum convexity at median constriction. Frontal lobe broadly pear-shaped, well-defined all round, posterior part enclosed by axial furrows which diverge forwards to enclose an angle of 50–70 degrees. These axial furrows continue backwards to form powerful, broad, deepened IP apodemes. Axial furrows again shallow posteriorly to continue as depressions between basal glabellar lobe and inflated genal lobes to meet lateral end of occipital furrow. Basal genal lobes fusiform, inclined inwards-forwards, and greatly inflated, extending forwards to a point near anterior edge of palpebral lobes. These basal lobes are mostly outside the area subtended by the occipital ring, and they are of extraglabellar origin, being produced by an adaxial inflation of the genal region. Occipital furrow transverse, and especially deep at either side; occipital ring of uniform width (sag., exsag.) deeply downcurved laterally to meet posterior border. Presumed axial furrows passing on outside of basal lateral glabellar lobes, diverging backwards, very shallow anteriorly and deepening to border furrow. Strong glabellar tubercle in front of occipital furrow. Palpebral lobes elevated to about the level of frontal glabellar lobe, small (about one-sixth glabellar length) and close to axial furrows, strongly curved to slightly more than a semicircle. Apparently narrow palpebral rims. Postocular cheeks acutely triangular, transverse width about half that of occipital ring, posterior border narrow (exsag.) and highly convex, as defined by a deep border furrow. Preocular sutural divergence somewhat exceeds that of anterior section of axial furrows so that the downward-sloping preocular cheeks, which are very narrow (tr.) in front of eyes, increase gradually in transverse width forwards. Sutures converge across anterior border, presumably running marginally to meet at mid-line. Border abruptly breaks downward slope of preocular cheeks, being flat to slightly concave with rounded rim. Anterior edges of border converge towards mid-line at a large obtuse angle, but rounded medially. Border furrow broad and diffuse; preglabellar field lacking.



TEXT-FIG. 6. *Norasaphus (Norasaphus) skalis* gen. et sp. nov. Reconstruction of cephalon and pygidium, $\times 1$.

EXPLANATION OF PLATE 39

Figs. 1–8. *Norasaphus (Norasaphus) skalis* gen. et sp. nov. Lower part of Nora Formation, loc. 071/4 (1, 3–8) and loc. 127/12 (2). 1, CPC 22653, holotype, well-preserved but slightly incomplete cranidium, $\times 6$. 2, CPC 22654, 22655, latex cast taken from external mould of two cranidia, $\times 4$. 3, CPC 22664 free cheek, plan view partly exfoliated, $\times 4$. 4, CPC 22656, latex cast from small cranidium from same bed as holotype, $\times 6$. 5, CPC 22661, incomplete large pygidium, showing surface sculpture, $\times 4$. 6, CPC 22662, small pygidium, excavated to doublure on right, $\times 6$. 7, CPC 22666, hypostoma, exfoliated, $\times 6$. 8, CPC 22663, large, exfoliated pygidium; dorsal surface sculpture is not reflected on the internal surface, and more axial rings are visible, $\times 3$.



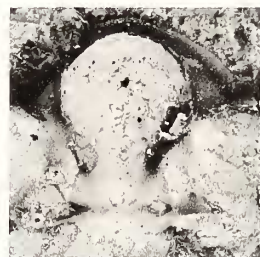
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Surface sculpture of tubercles and granules on glabella, occipital ring, and anterior rim. Tubercles sparse but large on posterior median lobe of glabella and occipital ring; these large tubercles reflected also on internal moulds, but pre-occipital glabellar tubercle exceeds all in prominence. Finer tubercles on frontal glabellar lobe, basal lobes, and fine granules on forward part of anterior border; these not reflected on internal moulds.

Free cheeks with long, slightly curved genal spine. Genal field convex (exsag.) with zone of tubercles surrounding base of eye but not extending anteriorly or laterally. Deep posterior border furrow narrows abruptly abaxially over region corresponding to inner margin of doublure. Lateral border continues from cranidium narrowing round periphery of cheek and passing on to genal spine, which thereby carries a groove down its exterior surface. Eye strip-like, slightly elevated from cheek on smooth socle. Doublure broad beneath genal fields, recurved beneath cheek well beyond border but narrowing as the suture is approached to form a comparatively narrow band extending anteriorly beneath cranial border to median suture. Deep vincular furrow about one-third length of lateral border on cheek, bounded by ridges on doublure. Terrace lines on ventral doublural surface not reflected on its dorsal surface.

Hypostomata of type consistently found with *Norasaphus*, and therefore associated with some confidence. Conventional asaphine type, similar to that of *Basiliscus*, for example, with subcircular middle body, ill-defined, carrying pair of forward-inclined, smooth maculae. Lateral borders wide, with maximum width at about half hypostomal notch with shape like inverted U. Terrace lines relatively fine and transverse on middle body, parallel to margins of borders.

Pygidium with sagittal length about twice maximum width, pleural fields convex, with steep downward slope to border. Axis occupying less than one-third pygidial width at anterior margin, and extending to posterior border, with rounded tip; gentle axial taper encloses angle of no more than 20 degrees. On specimens preserving cuticle two axial rings are clearly defined, separated by deep ring furrow. Ring furrows become faint after that defining second axial ring, definition of third and fourth rings poor, principally on flanks of axis. Internal moulds show up to seven faint rings. Articulating half-ring of similar (sag.) length as first axial ring. Dorsal surface shows four pairs of pleural furrows, the first of which extends to the border, the posterior three progressively shorter and further removed from border. Interpleural furrows divide the first three ribs just anterior to centre line, much shallower than pleural furrows, and not reflected on internal mould. Broad, triangular facet about twice transverse width of border. Border gently downsloping laterally, becoming progressively narrower and more steeply sloping posteriorly. Definition of border sharper on small specimens. Sculpture, mostly on axis and faint on pleural ribs, tubercles like those on glabella; few faint scalloped terrace lines on border.

Discussion. This is the only species attributed to *Norasaphus* (*Norasaphus*). Small cranidia show that the 'basal glabellar lobes' originate from an extra-glabellar position adjacent to the base of the glabella (Pl. 39, fig. 2). With increase in size they tend to migrate adaxially. In many Asaphinae the posterior part of the glabella tends to effacement, and in these circumstances it can be difficult to distinguish the 'glabellar' from the genal areas. The distinguishing asaphine feature appears to be the deepening of the axial furrows at what we have termed the IP position at the rear end of the frontal lobe, a feature which remains constant whatever the degree of effacement on the rest of the cranidium.

Subgenus *Norasaphites* subgen. nov.

Type species. *N. (Norasaphites) monroae* sp. nov.

Diagnosis. *Norasaphus* species with smooth or tuberculate exoskeleton. IP united across glabella to form definite transglabellar furrow. Pygidial border absent.

Derivation of name. Diminutive of *Norasaphus*.

Species included. *N. (Norasaphites) monroae* sp. nov., *N. (N.) vesiculosus* sp. nov.

Norasaphus (Norasaphites) monroae sp. nov.

Plate 40, figs. 1-4, 6-10; text-fig. 7

1980 Asaphid gen. nov.; Fortey, p. 256, fig. 2.

Diagnosis. *Norasaphus (Norasaphites)* species lacking surface sculpture; frontal glabellar lobe not greatly inflated; eyes strongly stalked. Pygidium tending to effacement on posterior part of axis and pleural lobes, with only three pairs of pleural furrows.

Derivation of name. Dedicated to Marilyn Monroe.

Holotype. Cranidium, CPC 22668, from loc. 158/9.

Other material. Cranidia, CPC 22669, 22804–22822; pygidia, CPC 22670–22672, 22833–22839; librigenae, CPC 22673, 22674; hypostomata, CPC 22675, 22676, 22843.

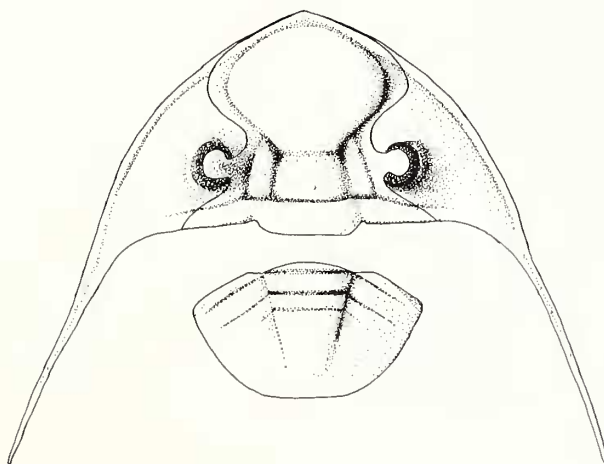
Occurrence. Upper part of Nora Formation, locs. 015/6, 122/1?, 158/4, 158/8, 158/9, 158/13, 158/15, 308/1.

Description. Cranidium of relatively low transverse convexity compared with other species of *Norasaphus*. Glabella well-defined, hardly inflated, width at narrow 'neck' slightly less than half maximum width at anterolateral corners. The narrowest part of glabella lies at about one-quarter length of pre-occipital glabella. Deep axial furrows converge forward gently to this point, in front of which they diverge markedly around forward lobe of glabella, enclosing an angle of 75–80 degrees. Front margin of glabella broadly rounded about mid-line. Transglabellar furrow straight, less deep than occipital furrow. Occipital ring not as wide (tr.) as widest part of glabella, and of length (sag.) only slightly less than that of posterior glabellar lobe. Axial furrows are shallower where defining lateral ends of occipital ring. Occipital furrow narrow, deep, and straight transverse. Inflated bacculae three times longer than wide, inclined gently inwards until cut off by forward expansion of glabella at a point a little in front of the transglabellar furrow. Palpebral lobes greatly elevated above level of rest of cranidium, such that the intraocular cheek is nearly vertical, and sited at about mid-cranidial length. Narrow (tr.) preocular cheeks also inward-inclined, with outline closely following that of forward glabella lobe. Anterior border of cranidium acuminate, almost flat, wider medially, and at lateral edges. Posterior cranidial border convex, pointed, extending laterally to a point just beyond that of anterior cranidial border. External surface of cranidium lacking tubercles. Small cranidia (sag. length 0.5 cm or less) differ from the larger ones in having less marked expansion of the frontal glabellar lobe, and the pre- and postocular sutures are also less divergent.

Free cheek generally like that of *N. (N.) skalis*, but lateral border furrow shallower, and the genal spine is much shorter, pointed, not curved. The posterior border furrow becomes completely effaced as it approaches the doublure. The eye is borne on a distinct stalk (Pl. 40, fig. 6), such that it must have projected above the level of the rest of the trilobite.

Hypostoma rather flat, anterior width (tr.) of middle body about two-thirds maximum width across broad wings. Lateral margins of wings converge backwards to almost pointed tips separated by wide, shallow fork. Middle body not well-defined posteriorly, tapering to forward edge of fork, with pairs of shallow maculae.

Pygidium about two-thirds as long as wide, convex. Axis occupies more than one-third of total pygidial width anteriorly, tapering posteriorly such that the axial furrows enclose an angle of 25–30 degrees, at the same time becoming less convex so that its tip is not clearly defined from the postaxial field. Only two narrow axial rings are defined across the mid-part of the axis, and the second of these is faint. Third and fourth rings faintly indicated laterally. Half-ring of about same width (sag.) as first axial ring. Pleural furrows relatively narrow, first two pairs almost reaching margin, third usually extending no more than half-way across pleural fields (very faint fourth pair suggested on some specimens). Broad facets extend close to axis. Small pygidia relatively more transverse, with axis better defined.



TEXT-FIG. 7. *Norasaphus (Norasaphites) monroecae* gen. et sp. nov. Reconstruction of cephalon and pygidium, $\times 1.5$.

Discussion. This species is distinguished from *N. (Norasaphites) vesiculosus* below. The relatively low convexity, strongly stalked eyes and lack of surface sculpture are features which contrast with *N. (N.) skalis* stratigraphically below it; if we are correct in proposing a derivation of *N. (Norasaphites) monroae* from this more generalized form, there should be a functional explanation for the changes. One suggestion is that *N. monroae* was adapted to shallow infaunal life. The relative smoothness, and loss of convexity on the frontal glabellar lobe would have reduced sediment resistance during burial, and the high-perched eyes would have protruded above the sediment surface even when the rest of the animal was completely concealed. By contrast, *N. (Norasaphites) vesiculosus* carries the morphological peculiarities (tuberculation, glabellar inflation) of *N. (Norasaphus) skalis* even further and it was presumably a surface dweller. So in this case the speciation events producing *monroae* on the one hand and *vesiculosus* on the other were by niche partitioning, presumably operating sympatrically or parapatrically.

Norasaphus (Norasaphites) vesiculosus sp. nov.

Plate 40, fig. 5; Plate 41; text-fig. 8

1969 *Proetus?* sp.; Gilbert-Tomlinson in Hill *et al.*, pl. O-V, figs. 5, 6.

Diagnosis. *Norasaphus (Norasaphites)* species with tuberculate surface sculpture, frontal glabellar lobe greatly inflated, often overhanging border; eyes not so elevated as *N. (Norasaphites) monroae*. Pygidium with three or four strong pleural ribs.

Derivation of name. Latin *vesiculosus*, 'covered in blisters'.

Holotype. Cranidium CPC 22677, from loc. 158/8-9.

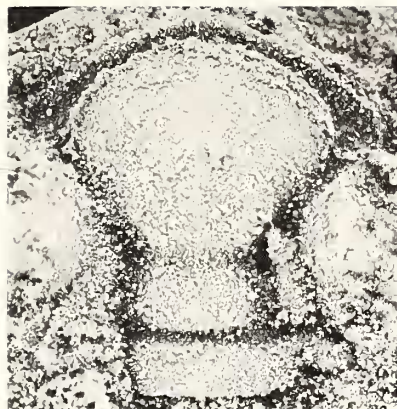
Other material. Cranidia, CPC 22678-22685, 22844-22857; pygidia, CPC 22686, 22687, 22858-22862; librigenae, CPC 22688, 22689, 22863-22865; hypostomata, CPC 22690, 22866.

Occurrence. Higher parts of Nora Formation, locs. 015/6, 122/1, 122/4, 126/1-7, 126/11, 139/4, 156/1, 158/4, 158/8, 158/9, 158/10, 308/1.

Discussion. This species is best discussed briefly in relation to *N. (N.) monroae*, from which it differs in the following features: (1) The frontal lobe of the glabella is subspherical rather than wedge-shaped. Especially in stratigraphically later examples this lobe becomes enormously inflated, often becoming extended into an almost conical protuberance. The frontal lobe overhangs the cranial border, which becomes very narrow medially, forming a convex rim. (2) The anterior divergence of the facial sutures is lower. (3) The glabella (and adocular part of the free cheek) carries a sculpture of tubercles, which are quite coarse on some specimens; internal moulds are smooth. (4) The bacculae do not slope inwards. (5) The palpebral lobes, although elevated, are not higher than the frontal glabellar lobe; the eye is not stalked. (6) The free cheek is acutely triangular, with a distinct, narrow lateral border, the border furrow continuing on to the genal spine as a groove. (7) The pygidium is similar to that of *N. (N.) monroae* in lacking a border, and only two axial rings are clearly defined, the posterior part of the axis being smooth except for faint lateral indications of two or three segments.

EXPLANATION OF PLATE 40

Figs. 1-4, 6-10. *Norasaphus (Norasaphites) monroae* subgen. et sp. nov. Loc. 158/9 (1, 2, 4, 6, 7, 9, 10), loc. 308/1 (3), and loc. 015/6 (8). 1, 2, 10, CPC 22668, latex cast from holotype, external mould of cranidium in dorsal (1), anterior (2), and oblique (10) views, $\times 6$. 3, CPC 22669, internal mould of cranidium, $\times 4$. 4, CPC 22670, latex cast from pygidium, external mould, $\times 6$. 6, CPC 22674, latex cast from fragmentary free cheek, to show stalked eye, $\times 6$. 7, CPC 22675, internal mould of hypostoma probably belonging to this species, $\times 6$. 8, CPC 22673, internal mould of free cheek, $\times 2$. 9, CPC 22671, latex cast of external mould of pygidium, $\times 6$. Fig. 5. *N. (N.) vesiculosus* subgen. et sp. nov. CPC 22690, loc. 158, internal mould of hypostoma, $\times 6$. Fig. 11. Asaphid gen. et sp. indet. CPC 22770, lowest Nora Formation, loc. 071/4, pygidium, $\times 6$.



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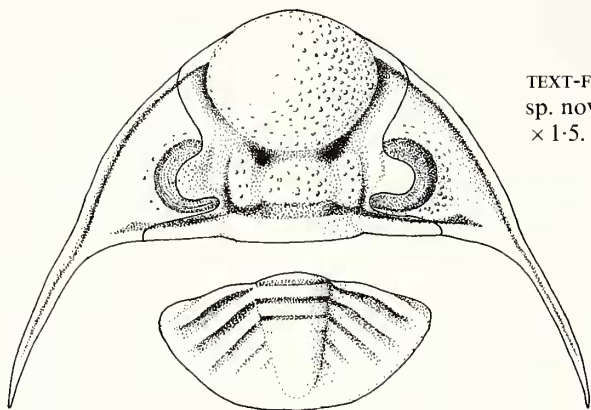
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TEXT-FIG. 8. *Norasaphus* (*Norasaphites*) *vesiculosus* gen. et sp. nov. Reconstruction of cephalon and pygidium, about $\times 1.5$.

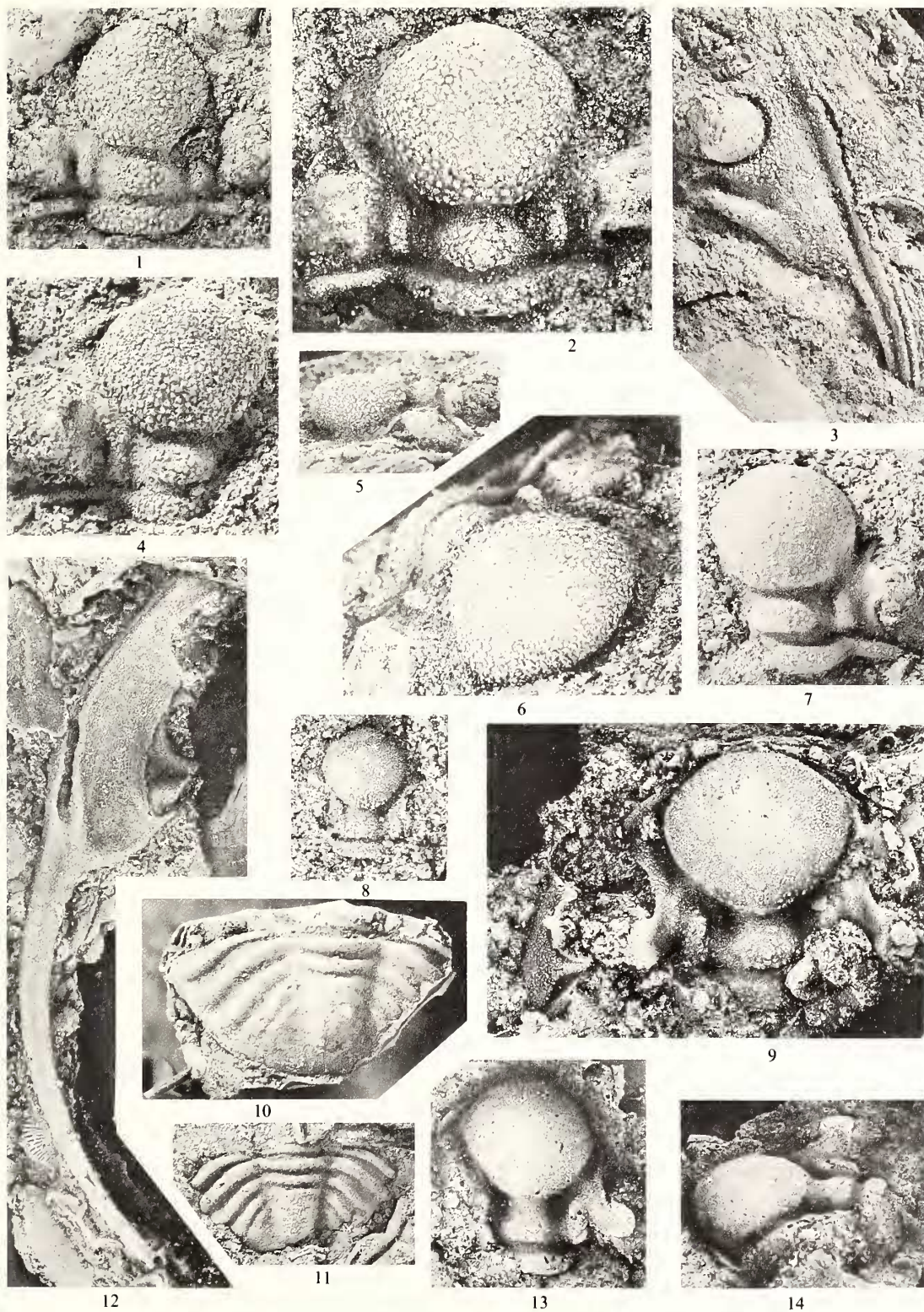
However, the tip of the axis is defined close to the posterior margin, and the pleural furrows are broad and deep, with the first three pairs running close to the margin and the fourth to about two-thirds the extent of the anterior pairs. There remains only a small, smooth triangular area adjacent to the posterior part of the axis. The areas between the pleural furrows, and between the first pair of furrows and the facets, are elevated into distinct ribs, which die out shortly before the pygidial margin. We have not, however, detected coarse granulation on the pygidial axis.

We admit a great deal of intraspecific variation in our concept of *N. (N.) vesiculosus*. This particularly relates to the development and sculpture of the anterior glabellar lobe. In some specimens this lobe is only about one and a half times the width (tr.) of the posterior glabellar lobe, in others fully twice as wide (Pl. 40, fig. 2); the inflation of the lobe varies also, some specimens becoming almost pointed. The coarseness of the tuberculation is variable: some specimens are coarsely tuberculate all over the glabellar lobes, others grade into fine granulation over the mid-part of the anterior lobe (Pl. 41, fig. 9). The more finely tuberculate form is associated with a free cheek which carries a longer, more curved genal spine than the typical form, which is that shown on the reconstruction in text-fig. 8.

The more inflated form seems to come from higher in the Nora Formation than the granulose form. However, there appears to be every transition between these various morphs and, for this reason, we take a taxonomically conservative view and incorporate them within a single species. The great variability is presumably another indication of the processes of endemic speciation at work, and would repay study with larger populations than we have available.

EXPLANATION OF PLATE 41

Figs. 1-14. *Norasaphus* (*Norasaphites*) *vesiculosus* subgen. et sp. nov. All latex casts from external moulds. 1, CPC 22678, loc. 308/1, cranidium of morph with pointed frontal glabellar lobe, $\times 4$. 2, 5, 6, CPC 22677, loc. 158/8-9, holotype in dorsal (2), anterior (5) ($\times 6$), and lateral (6) ($\times 3$) views. 3, CPC 22688, loc. 308/1, free cheek; note sculpture around base of eye, $\times 4$. 4, CPC 22679, loc. 308/1, cranidium of morph with especially expanded (tr.) frontal glabellar lobe, $\times 6$. 7, CPC 22680, loc. 122/4, cranidium of morph with relatively subdued tuberculation, but glabellar proportions like holotype, $\times 3$. 8, CPC 22681, loc. 126/3, small cranidium, $\times 3$. 9, CPC 22682, loc. 126/7, cranidium, with incomplete free cheek on left; this is the morph with expanded frontal lobe (as fig. 4), but with frontal lobe granulate rather than tuberculate, and somewhat elevated palpebral lobes, $\times 3$. 10, CPC 22686, loc. 308/1, pygidium, $\times 2$. 11, CPC 22687, loc. 015/6, incomplete pygidium, showing granulation on terminal piece of axis, $\times 2$. 12, CPC 22689, loc. 126/7, free cheek associated with the sparsely tuberculate morph, same locality; cast taken to show ventral surface with doublure and vincular notch, $\times 3$. 13, 14, CPC 22683, loc. 126/7, cranidium of sparsely tuberculate morph, dorsal (13) and lateral (14) views, $\times 3$.



FORTEY and SHERGOLD, *Norasaphus* (*Norasaphites*)

Subfamily ISOTELINAE Angelin, 1854

Genus *Fitzroyaspis* Legg, 1976

Type species. Priceaspis (Fitzroyaspis) guppyi Legg, 1976.

Discussion. Effaced asaphids are always a problem to classify, and the new species from the Nora Formation, described below, is no exception. Its few distinctive characters include a well-defined cephalic border, rounded genal angles, large medially placed eyes, and low sutural divergence behind the eyes. The pygidium is characteristically asaphid, but with no particularly distinctive features. Few asaphids have facial sutures that are not highly divergent behind the eyes, and of those with weakly divergent sutures (e.g. *Asaphellus*) most have small eyes and long genal spines. *Isotelus* itself has generally smaller eyes, the cephalic border is ill-defined, and the pygidium is characteristically triangular in outline; any resemblance between this typically North American genus and the Australian form is because of convergence. The same probably applies to such genera as *Anataphrus* and *Homotelus* in which effacement has gone even further; these genera lack defined cranial borders altogether, although the general cranial outline of certain species of *Anataphrus* is like that of our material. Legg (1976) described the type species of *Priceaspis (Fitzroyaspis)* from the early Arenig of the Canning Basin. The general cephalic structure is like our species, especially with regard to the well-defined, but narrow cephalic border. The pygidial border is comparatively poorly defined, a difference we do not consider of generic importance. The major point of difference lies in the more posterior extension of the eyes in *F. guppyi*, with a concomitant high angle of postocular suture divergence, and the presence in that species of distinct posterior border furrows. The cranidium of our species is also somewhat broader in proportion to its length. We regard these differences as of specific significance only, effectively produced by an anterior migration of the eyes compared with *F. guppyi*. A similar 'trend' happens also in *Isotelus* comparing the position of the eyes and sutural form in *I. copenhagenensis* Ross and Shaw (1972, pl. 2, fig. 8) with *I. gigas* Dekay. Legg separated *Fitzroyaspis* as a subgenus of his relatively uneffaced genus *Priceaspis*; with the inclusion of a second species in *Fitzroyaspis* we prefer to accord it full generic status until the phylogenetic relationships of these asaphids can be fully worked out.

Fitzroyaspis irritans sp. nov.

Plate 42, figs. 1–4, 7; text-fig. 9

Diagnosis. Highly effaced *Fitzroyaspis* lacking cephalic posterior border furrows; eyes smaller than in *F. guppyi*; postocular sutures divergent at a low angle; pygidium with border expressed laterally.

Derivation of name. Latin *irritans*, 'irritating', referring to the problem of its generic assignment.

Holotype. Cranidium, CPC 22691, from loc. 158/10.

Other material. Cranidia, CPC 22692, 22867–22878; hypostomata, CPC 22697, 22888; librigenae, CPC 22693, 22694, 22879–22881; pygidia, CPC 22695, 22696, 22882–22887.

Occurrence. Through most of higher Nora Formation, locs. 122/4, 126/7, 158/4, 158/10, 158/15.

EXPLANATION OF PLATE 42

Figs. 1–4, 7. *Fitzroyaspis irritans* sp. nov. Middle to upper Nora Formation. 1, CPC 22697, loc. 158/4, latex cast of hypostoma most probably belonging to this species, $\times 3.5$. 2, CPC 22691, loc. 158/10, latex cast taken from holotype, external mould of cranidium, $\times 2$. 3, CPC 22693, latex cast taken from external mould of free cheek, $\times 2$. 4, CPC 22694, loc. 158/15, free cheek, prepared to show doubleure and vincular furrow, $\times 3$. 7, CPC 22695, loc. 126/7, latex cast from external mould of pygidium, $\times 4$.

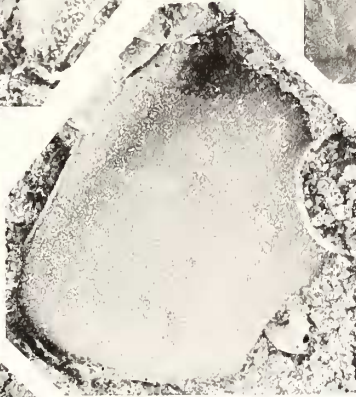
Figs. 5, 6. *Presbrynileus* cf. *P. utahensis* Hintze, 1953. Upper Nora Formation. 5, CPC 22710, loc. 308/1, internal mould of cranidium, $\times 3$. 6, CPC 22712, loc. 158/11, internal mould of pygidium, $\times 3$.



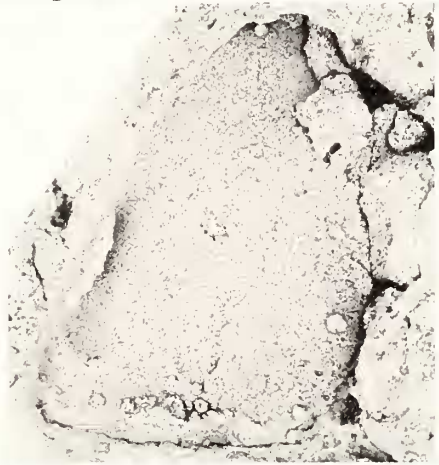
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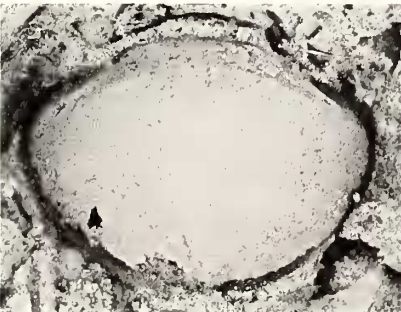
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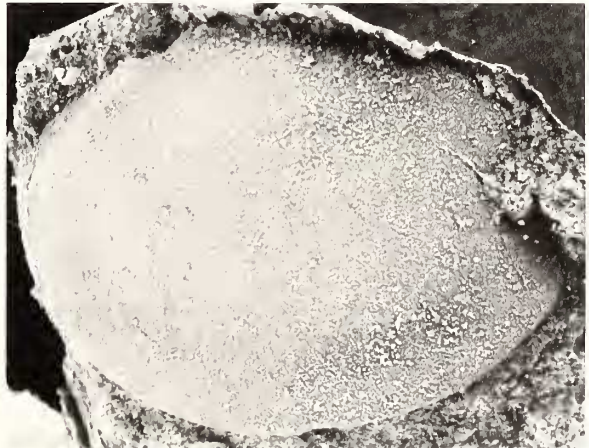
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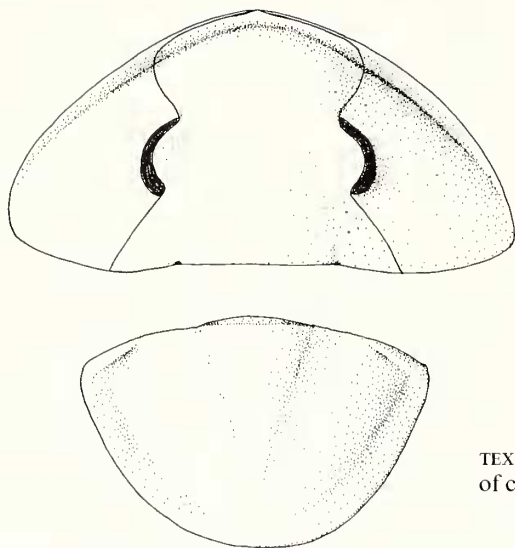
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TEXT-FIG. 9. *Fitzroyaspis irritans* sp. nov. Reconstruction of cephalon and pygidium, $\times 1$.

Description. Cranidium with width across palpebral lobes 0.85 of sagittal length on large cranidia; small cranidia tend to be more elongate. Very low convexity across the axial region suggesting glabella forward-tapering from prominent articulating notches at posterior margin, opposite hind ends of palpebral lobes. Steep downturn around frontal glabellar lobe and in front of palpebral lobes on to virtually flat cranial border, which does not exceed one-eighth (and may be as little as one-tenth) of the total glabellar length at mid-line. Palpebral lobes medially placed, tilted only slightly upwards, and with length (exsag.) one-third glabellar length. Facial sutures distinctly isoteliform, diverging at a low angle (20–40 degrees) in front of the eyes, and at a scarcely higher angle behind the eyes. The gently downsloping, triangular postocular cheeks so defined terminate acutely. Internal moulds show prominent glabellar tubercle (not visible externally) placed at about one-quarter glabellar length. Also some internal moulds show what are probably prominent 1P muscle impressions constricting the glabella shortly in front of the tubercle. Small cranidia of sagittal length 1 cm or less have more divergent sutures in front of and behind the eyes, but the fixed cheeks do not become extended (tr.) in the manner of *F. guppyi*. We tentatively associate a hypostoma (Pl. 42, fig. 1) of typical isoteline type, which does not belong to *Norasaphus*, and is from the same bed in which *F. irritans* is common.

Free cheek somewhat longer (exsag.) than wide in plan view, showing border becoming narrower and feebler towards the broadly rounded genal angle. On doublure vincular furrow runs parallel to border.

Pygidium two-thirds as long as wide, with gently convex pleural fields sloping down to ill-defined, still sloping border, which peters out around tip of axis. Pleural fields unfurrowed. Axis extends to more than two-thirds pygidial length; on the external moulds no ring furrows are visible, but on internal moulds four (?five) rings may be visible, of which only the first two are defined across the mid-part of the axis. Doublure broad, and concave towards outer edge, carrying at least twenty terrace lines which are approximately parallel to the posterior margin peripherally but slope backwards at a much more acute angle to the sagittal line near inner edge of doublure. Lateral tip of doublure sharply downward-flexed.

Discussion. *F. irritans* is distinguished from *F. guppyi* by its smaller eyes and wider cranidium, and by the low angle of divergence of the facial sutures behind the eyes; the pygidial border of the new species is better defined. In addition to the genera discussed above there is a certain resemblance between the cranidium of *F. irritans* and that of *Ptyocephalus*, especially *P. accliva* (Hintze 1953, pl. 15, fig. 2). However, the important features of *Ptyocephalus* are outside the axial region—a compression of the lateral pleural area resulting in laterally truncate free cheeks and pygidium.

Genus *Lycophron* gen. nov.

Type species. *Lycophron rex* sp. nov.

Diagnosis. Large, effaced isotelines with elongate, triangular cephalon and pygidium. Cephalon with

extremely narrow, acute lateral borders. Pygidium usually lacking border altogether. Hypostoma narrow (tr.) anteriorly, with very long fork with pointed tips.

Derivation of name. After the third-century Greek philosopher Lycophron.

Discussion. This genus resembles *Megistaspidella* and *Isotelus*. It is convergent upon both, but we believe that there is no phylogenetic connection. *Megistaspidella* is confined to the Baltic continent in the early middle Ordovician, and is related to the *Megistaspis* plexus of species. Its pointed, unforked hypostoma lies at the opposite morphological extreme among asaphids to that of *Lycophron*, and is sufficient evidence of their separate origins. *Isotelus* includes some species, such as *I. gigas*, which are like *L. rex*. These *Isotelus* species are much younger than the Australian genus. Early representatives of *Isotelus*, such as *I. harrisi* (see Shaw 1968, pl. 22), are quite different, with relatively broad cephalic and pygidial borders, and wide lateral borders on the hypostoma. These in turn are related to the early middle and early Ordovician genera *Stegnopsis* and *Isoteloides* which are unlike *Lycophron* in almost every particular, although they are its North American contemporaries. So in our view *Isotelus* species resembling *Lycophron* were independently derived later in the Ordovician (see also *Lycophron* sp. A below). The hypostoma of the *Isotelus*-*Isoteloides* group remains generally conservative, with broader borders than in *Lycophron*, and flared tips to the fork. The pygidial border is visible in *Isotelus*. The similarities between *Lycophron*, *Isotelus*, and *Megistaspidella* probably indicate similar life habits in response to a comparable environment: all are found in calcareous, epicratonic sediments.

Species included. *L. rex* sp. nov., *Asaphus howchini* Etheridge, 1894, *L. sp. A* (below).

Lycophron rex sp. nov.

Plate 43, figs. 1–10; text-fig. 10

Diagnosis. As for genus.

Derivation of name. Latin *rex*, 'king', for the largest of the Nora trilobites.

Holotype. Pygidium, CPC 22698, from loc. 126/5.

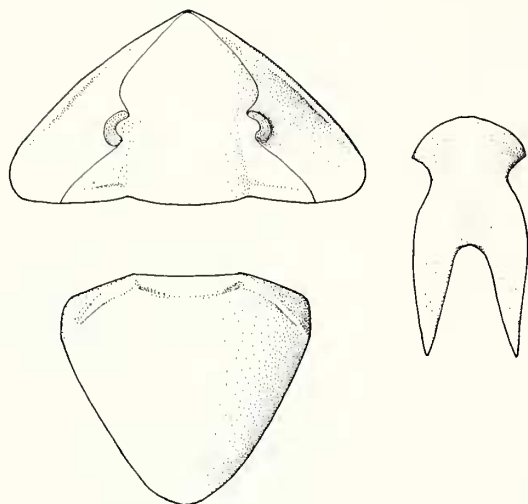
Other material. Cranidium, CPC 22699; librigenae, CPC 22700, 22701, 22889–22891; hypostomata, CPC 22706, 22707, 22897, 22898; pygidia, CPC 22702–22705, 22892–22896.

Occurrence. Ranges throughout the Nora Formation except the basal part: at locs. 118/7, 122/1, 122/3, 126/1, 126/2, 126/3, 126/5, 127/7, 127/12, 152/9, 308/1.

Description. One or two large hypostomata, and pygidial fragments, indicate that this species grew to a considerable size. Most pygidia are 1–2 cm long, and the description is based on material of this size. Pygidia are abundant in the Nora Formation; cranidia are distinctly rare. There does not seem any reason to doubt that the association is correctly made. Disparity between the numbers of pygidia and cranidia preserved is rather common among asaphids; possibly the irregularly shaped cranidium was susceptible to fracture during post-mortem current sorting compared with the compact pygidium.

Cranidium with outline generally like isosceles triangle; relatively long and pointed anterior 'nose' distinctly convex transversely, while there is a gentle downward slope on the posterior fixigenae. Glabella defined by shallow furrows converging forwards to pass well inside palpebral lobes; anterior course of axial furrows not well-marked, but they appear to swing out towards the posterior margin of the frontal cranidial lobe. There was probably a faintly defined occipital ring, incompletely preserved on our material. Small palpebral lobes slightly elevated, and in relatively forward position for an asaphid at about mid-cranidial length. Acute triangular postocular cheeks defined by sutures which run in a nearly straight course to the posterior margin. Border furrow relatively deep, especially near glabella. Slight tendency towards flattening of anterior, pointed part of cranidium.

Long and acutely triangular free cheeks are assigned to this species, having the eye in the appropriate advanced position, and lacking genal spines. There is a narrow border, having a narrow and steep exterior face, and topped by an acute rim; border furrow at its mid-length, but fading out before the genal angle, and also anteriorly. A sharp vincular notch truncates the outside face of the border near the genal angle, where the border furrow fades out.



TEXT-FIG. 10. *Lycophron rex* gen. et sp. nov.
Reconstruction, $\times 1$.

Hypostoma remarkably long and narrow, looking like a tuning fork. Anterior margin bowed forwards. Front part of hypostoma narrower (tr.) than width at front end of fork. The fork itself is so deep that the prolongations on either side are more than twice, or even three times, as long as wide. Middle body does not seem to be defined on our specimens, the whole of the posterior part of the hypostoma forming an almost flat plane. The large examples, which almost certainly belong to this species, have a broader, less acute fork, and a pair of faint depressions represent the maculae.

Deeply convex (tr.) pygidia are typically triangular, with an acute tip slightly rounded, and with width equal to, or slightly exceeding, the sagittal length. There is no sign of axis or border, although the width of the former at the front margin is indicated by a distinctly defined, fusiform half-ring occupying 0.4 of maximum pygidial width. The broad (tr.) articulating facets are backed by convex half-ribs, and a single pair of deep but narrow pleural furrows which do not extend to the pygidial margin. Doublure narrow for an asaphid, gutter-like. The combination of long, triangular shape, high effacement, yet deep furrows on the anterior segment only makes these pygidia distinctive compared with most asaphids. Some specimens (Pl. 43, fig. 8), from stratigraphically high in the range of the species, are relatively even more elongate and tend towards flattening of the posterior tip of the pygidium. We do not have enough specimens to know whether this is a consistent difference deserving taxonomic recognition. There is no indication of surface sculpture in this species, apart from terrace lines on doublure and hypostoma.

Discussion. Etheridge (1894) described *Asaphus (Megaspis) howchini* from the MacDonnell Ranges, figuring a large pygidium with attached thoracic segments, very similar to *L. rex* and undoubtedly congeneric. A similar pygidium from the Nora Formation was figured by Gilbert-Tomlinson (*in Hill et al.* 1969, pl. O-V, fig. 4). Etheridge's original specimen is refigured here as text-fig. 11. The pygidial axis is defined, whereas all specimens of *L. rex* are completely effaced. Even small (3 mm long) pygidia

EXPLANATION OF PLATE 43

Figs. 1-10. *Lycophron rex* gen. et sp. nov. Middle to upper Nora Formation. 1, CPC 22700, loc. 118/7, latex cast from free cheek, $\times 3$. 2, 3, CPC 22699, loc. 158/4, cranium in dorsal (2) and lateral (3) views, $\times 2$. 4, CPC 22702, 22703, loc. 126/2, latex cast showing two pygidia, $\times 2$. 5, CPC 22706, latex cast of hypostoma, same bed as holotype, $\times 6$. 6, 10, CPC 22698, loc. 126/5, holotype, latex cast of large pygidium in dorsal (6) and oblique lateral (10) views, $\times 5$. 7, CPC 22704, loc. 127/7, pygidium, relatively short compared with other examples, $\times 10$. 8, CPC 22705, loc. 308/1, pygidium, most elongate form in which the tip shows tendency to become spatulate, $\times 3$. 9, CPC 22701, loc. 158/4, cast from free cheek, $\times 2.5$.

Figs. 11, 12. *Lycophron* sp. A. CPC 22708, lower Nora Formation, loc. 071/4. Pygidium in dorsal (11) and posterior (12) views, $\times 6$.



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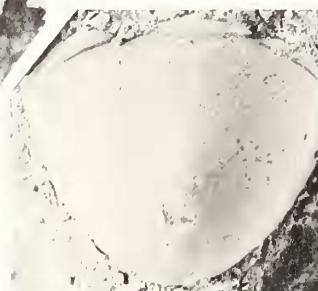
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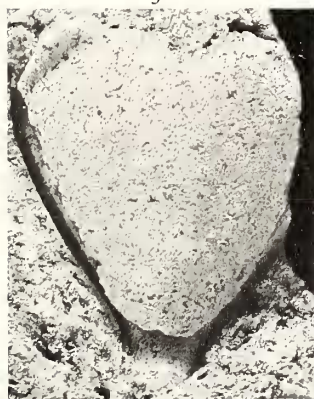
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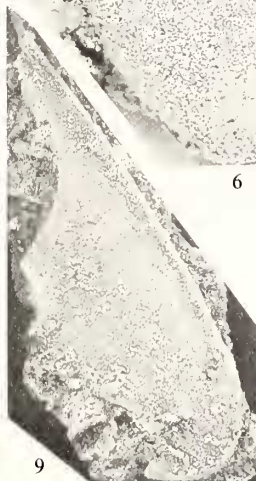
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12



TEXT-FIG. 11. *Lycophron howchini* (Etheridge), South Australian Museum type collection, F 7104. Lectotype thorax and pygidium, $\times 0.5$.

of *L. rex* show no indication of the pygidial axis; definition of dorsal furrows in asaphids is usually more marked in smaller specimens. So the difference between *L. rex* and *L. howchini* is real, and unlikely to be because of a difference in preservation or size. Etheridge (1894, pl. 3, fig. 2) figured an asaphid hypostoma, which is very likely that of *L. howchini*. A species which may prove to be *L. howchini* occurs commonly in the Carlo and Mithaka Formations overlying the Nora Formation in the Georgina Basin.

Lycophron sp. A

Plate 43, figs. 11, 12

Material. Pygidia, CPC 22708, 22709, from loc. 071/4.

Occurrence. Lowest part of Nora Formation, loc. 071/4.

Discussion. A second species of *Lycophron* is represented by pygidia only, occurring stratigraphically beneath *L. rex*. We cannot formally name it on the basis of this sparse material. It differs from the type species in having a well-defined pygidial axis extending almost to the posterior margin, furrowed pleural fields and a distinct border, but it shares the distinctive triangular shape. At least fifteen pairs of muscle impressions are visible on the flanks of the pygidial axis, and ten or eleven segments are expressed on the pleural fields, represented by shallow pleural and interpleural furrows which stop at the border. Like *L. rex*, only the first pair of pleural furrows are deep. The pygidium is more transverse than that of *L. rex* or *L. howchini*, and the latter also has unfurrowed pleural fields and no border. Presumably *L. sp. A* shows the primitive condition in *Lycophron*—furrowed pleural regions and pygidial borders are primitive for the Asaphidae as a whole. Note that this pygidium is unlike that of *Isoteloides* (from which *Isotelus* was probably derived) and *Megistaspis* (a close relative, if not the ancestor of *Megistaspidella*) which may be taken as evidence that any resemblance between *Lycophron* and *Isotelus* or *Megistaspidella* is a matter of convergence rather than phyletic relationship.

Genus *Presbynileus* Hintze, 1954

Type species. *Paranileus ibexensis* Hintze, 1953, by original designation.

Presbynileus cf. *P. utahensis* (Hintze, 1953)

Plate 42, figs. 5, 6

Material. Cranidia, CPC 22710, 22899–22903; pygidia, CPC 22712, 22713, 22904, 22905.*Occurrence.* Mid to upper parts of the Nora Formation, locs. 038/38, 126/7, 158/9, 158/11, 308/1.

Discussion. This highly effaced asaphid is quite frequent in the higher part of the Nora Formation; cranidia are immediately distinguishable from those of *Fitzroyaspis irritans* in lacking a border. The cranidium has medially placed palpebral lobes and very short (tr.) postocular cheeks, defined by distinctly curved sutures. The pygidium assigned here also lacks all traces of a border. *Presbynileus* includes several species from the early Ordovician of Utah which agree with the Nora material in their salient features; only one of these, *P. utahensis*, has convex postocular sutures and narrow cheeks like our species. Hintze's (1953, pl. 13, fig. 2) cranidia are only about 0.5 cm long, whereas we have specimens up to 2 cm long. We can see no points of difference between the type cranidium and that illustrated on Plate 42, fig. 6, other than slightly shorter palpebral lobes in the Nora form (which could well be accounted for by difference in growth stage). Pygidia are of similar dimensions, although the axis of the Nora form is wider. We have not recovered a hypostoma from the Nora Formation. The similarities between material from these widely separated localities are sufficient to suggest conspecificity. We retain a qualification to cover the pygidial difference, and because we have not yet recovered the distinctive hypostoma from Australia.

Asaphid gen. et sp. indet.

Plate 40, fig. 11

Material. Pygidium, CPC 22711.

Discussion. One or more asaphids additional to those described above occur in the Nora Formation; they are fragmentary and difficult to associate, and no formal nomenclature is possible. The pygidium illustrated is from the lower Nora Formation at 071/4. It is similar to that of a species described by Legg (1976) as *Asaphellus pricensis* from the Canning Basin, except that the pygidial axis is somewhat longer in our form.

Family DIKELOKEPHALINIDAE Kobayashi, 1936

Genus *Hungioides* Kobayashi, 1936*Synonymy.* *Argentinops* Přibyl and Vaněk, 1980, p. 38, fig. 11.*Type species.* *Dikelokephalina bohémica* Perner, in Novák and Perner 1918, by original designation.

Discussion. Lu (1975, p. 357) has discussed the definition of genera in the Dikelokephalinidae. He cites the presence of two pairs of pygidial spines as diagnostic of *Hungioides*. Material from the Nora Formation should be placed in *Hungioides* on the basis of this character. However, Lu also regards a 'bell-shaped glabella with rounded frontal lobe' as typical, whereas the Australian material shows a conical forward part of the glabella, in this respect resembling certain *Asaphopsis* species, or *Asaphopsoides*. In the family as a whole there appears to be a good deal of variation in glabellar shape between species, as there is in incision of glabellar furrows, and we regard the pygidial structure as the better generic discriminant in this case. Přibyl and Vaněk (1980) distinguished the genus *Argentinops* (based on *Asaphopsis intermedia* Harrington and Leanza) on the basis of its more slender exterior pair of pygidial spines. This is scarcely adequate for generic discrimination, and may be subject to ontogenetic variation as well; hence we regard *Argentinops* as a subjective synonym of *Hungioides*.

Hungioides acutinasus sp. nov.

Plate 44

Diagnosis. *Hungioides* with conical glabellar front; highly divergent preocular facial sutures;

palpebral lobes half glabellar length (including occipital ring). Pygidial spines relatively slender compared with other species.

Derivation of name. Latin *acutinasus*, 'sharp-nose', referring to the shape of the glabella.

Holotype. Cranidium, CPC 22714, from loc. 126/3.

Other material. Cranidia, CPC 22715, 22716, 22906–22908; pygidia, CPC 22717–22720, 22909–22915; probable librigenal fragment, CPC 22721.

Occurrence. Lower to upper Nora Formation, locs. 071/4, 122/1, 126/1, 126/3, 126/4, 126/5, 126/11, 152/9, 158/4, 308/1.

Description. This species must have attained a large size. Cranidia probably attained a length of about 4 cm and a width of at least 6 cm; pygidia were over 4.5 cm long (including spines); complete specimens probably exceeded 12 cm in length. The well-preserved cranidia are all small, 2 cm long or less, and the description is mostly based on these. The general convexity of this species is remarkably low: the highest parts of the cranidium are the glabellar mid-line and the palpebral lobes, the latter being quite elevated, which would result in the visual surfaces on the free cheeks being higher than most of the rest of the exoskeleton. Glabella with maximum width at occipital ring, being 0.7 sag. length. Gentle forward taper increases greatly at level of 3P glabellar furrows, such that the front part is broadly conical, although rounded medially. Occipital ring well-defined, furrow shallower medially, deepened slightly on line with inner ends of glabellar furrows. Three pairs of glabellar furrows, isolated as pits within glabella: 1P forked at inner end, the posterior branch of fork especially strong; 2P and 3P close together, broadly oval (tr.), 3P placed opposite forward end of palpebral lobe. Distance between 2P and 3P approximately half that between 2P and 1P and between 1P and the occipital furrow. Furrow circumscribing glabella uniformly narrow and shallow. Prominent 'alae' are here semicircular, depressed areas about half as long as the palpebral lobes and with hind ends adjacent to the occipital furrow. Palpebral lobes large (measured exsag. about half total glabellar length), and posteriorly placed such that the posterior ends are behind the occipital furrow; hence the postocular cheeks are reduced to very narrow strips. Divergent anterior sections of the facial sutures are broadly sigmoidal, mid-section making an angle of 45–60 degrees with sag. line on smaller cranidia; on a large, fragmentary specimen this angle has increased to more than 80 degrees, resulting in an extremely wide (tr.) preglabellar area. Paradoxiblural line meets the preocular suture at about its mid-length. This line serves to divide posterior depressed area from the very gently convex preglabellar/anterolateral field, which widens towards the exsagittal part of glabella. Broad, depressed border furrow separates this convex area from narrow, distinctly upturned brim.

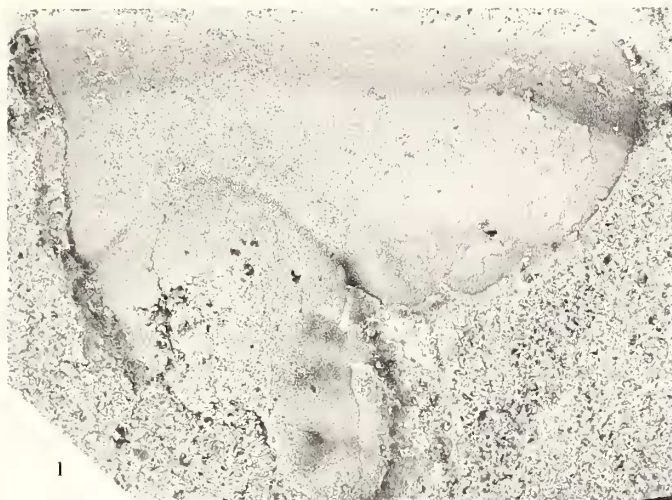
As far as preserved, the cuticle on this large species was very thin. The biggest specimen preserves traces of some terrace lines running approximately parallel with the anterior margin across the preglabellar field and border.

Pygidia are mostly fragmentary, but several prove the existence of two pairs of marginal spines. The narrow axis tapers uniformly backwards to more than half pygidial length, and is continued into a postaxial ridge which does not extend on to the border (the exact tip of the axis is thus hard to discern). Up to seven axial rings are present, of which the first four are well-defined. Ribs number six, adaxial parts sloping progressively backwards posteriorly; they fade out on inner part of concave border, which had terrace lines like those on the cephalic border. On large pygidia the marginal spines are slender, and the exterior pair are about as long as the pygidial axis. A well-preserved, small pygidium (Pl. 44, fig. 6), which is probably referable to *H. acutinasus*, shows a relatively broad (tr.) outer pair of spines, and it seems likely that these became more slender during later ontogeny.

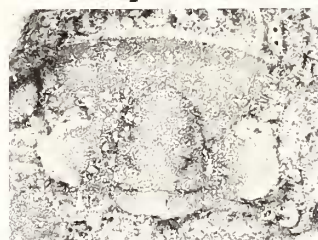
Discussion. The type species (Novák and Perner 1918, pl. 1, figs. 4, 6; Marek, *in* Horný and Bastl 1970, pl. 5, fig. 7) from the Llanvirn Šarka Formation of Bohemia, has a pygidium with at least eleven axial

EXPLANATION OF PLATE 44

Figs. 1–7. *Hungioides acutinasus* sp. nov. 1, CPC 22715, loc. 126/3, fragment of large exfoliated cranidium, $\times 2$. 2, CPC 22714, loc. 126/3, holotype cranidium, internal mould, $\times 3$. 3, CPC 22716, latex cast of small cranidium, same bed as holotype, $\times 3$. 4, CPC 22721, locality as holotype, incomplete free cheek probably belonging here, internal mould, $\times 3$. 5, CPC 22717, loc. 126/5, latex cast from incomplete, large pygidium, $\times 2$. 6, 7, CPC 22718, loc. 071/4, latex cast from well-preserved smaller pygidium (6), $\times 6$; and sculptural detail (7), $\times 12$.



2



3



4



5



7



6

rings, and a more prominent, stubbier interior pair of marginal spines. If the cranidium of *H. bohemicus* (Novák and Perner 1918, pl. 1, fig. 6) is correctly assigned, it has a more uniformly parabolic glabella and eyes further forward than in *H. acutinasus*. *H. graphicus* Richter and Richter, 1954, is generally similar to *H. bohemicus*, and differs from our species in the same pygidial features. Kobayashi (1936) separated the original pygidium of Novák and Perner (1918, pl. 18, fig. 5) as *H. novaki*; the marginal spines of this species are subequal in length, short and wide, and conjoined at their bases. The same kind of pygidial structure is shown by *H. mirus* Lu (1975, pl. 29, figs. 8–15). Both differ from *H. acutinasus* in the prominent development of the interior pair of spines, and the broad bases of the exterior ones. Cephalic characters of the Chinese species show that the eyes are in a similar posterior position to those of our species, but the anterior branches of the facial sutures are less divergent, and there is apparently no cranial border. Another species described by Lu (1975), *H. constrictus* from the Tremadoc, has a truncate glabella, smaller eyes, less divergent sutures, and an ill-defined border compared with *H. acutinasus*. '*Asaphopsis*' *intermedia* Harrington and Leanza, 1957, from the Llanvirn of Argentina also shows a small inner pair of pygidial spines, and is better referred to *Hungioides*. As in *H. acutinasus* the outer pair of spines are slender, but originate more adaxially. Apart from being more convex, the Argentine species has a pygidium with eleven axial rings and seven or eight pleural ribs. Přibyl and Vaněk (1980) erected a new genus, *Argentinops*, based on this species, which we consider to be a junior subjective synonym of *Hungioides*. The new species is thus readily distinguished from all others, but differences concerning sutural divergence and pygidial spines are not of generic significance.

Hungioides has a curious distribution. It extends from that part of Europe which was part of the *Selenopeltis* (high latitude) province through central and south-western China (also South America) to platform Australia, which as we have discussed was probably near the palaeoequator in the earlier Ordovician. Its thin cuticle, flattened form, and large size argues for benthic habits. This distribution is the only one known to us which shows independence of palaeolatitude at the generic level. The distribution does, however, appear to be peri-Gondwanan, but the genus is only at all common on the eastern part of its geographic range.

Family TELEPHINIDAE Marek, 1952

Discussion. We follow here the expanded concept of the Family Telephinidae introduced by Fortey (1975). The family includes five genera which had pelagic habits: *Carolinites* Kobayashi, *Telephina* Marek, *Goniophrys* Ross, *Oopsites* Fortey, and *Phorocephala* Lu (= *Carrickia* Tripp, 1965, see below).

Genus *Phorocephala* Lu, 1965

Type species. *Phorocephala typa* Lu, 1965, by original designation.

Discussion. The generic name *Phorocephala* has publication priority over *Carrickia* Tripp, 1965 (see Tripp 1976, p. 423). The type species of both genera are so similar that it is likely that both should be referred to the same genus, *Phorocephala*. *Phorocephala* species are distinguished from those of *Goniophrys* by their long (tr.) anterior cranial borders, and relatively gently curved palpebral lobes (Fortey 1976, fig. 11). The species from the Nora Formation is an early one, and retains a few features suggestive of derivation from *Goniophrys*.

Phorocephala sp. aff. *P. genalata* Lu, 1975

Plate 45, figs. 1–6

Material. Cranidia, CPC 22722–22724; pygidium, CPC 22725.

Occurrence. Lower part of Nora Formation, locs. 071/4, 127/3?.

Description. Glabella highly vaulted above fixed cheeks, maximum width being half that of cranidium measured transversely at back end of palpebral lobes. The glabellar outline is broadly parabolic, much like that of *Oopsites* or *Goniophrys*. Muscle impressions are lacking, except for a vague indication of 1P isolated within the glabella opposite hind part of palpebral lobes. Occipital ring about one-fifth total glabellar length. Axial and preglabellar

furrows uniformly deep around perimeter of glabella, but deepened into a pit anteromedially. Preglabellar field short, hardly downward sloping, merging without a sharp break into flat or gently concave border, the two together having about the same length (sag.) as that of the occipital ring when viewed dorsally. Lateral part of the preocular fixed cheeks steeply declined, so that the front edge of the cranidium is broadly upward-arched about the mid-line. Palpebral lobes of length 0.4 that of glabella (sag.), narrow and slightly convex, forward two-thirds curving gently inward-forward, posterior third curved inward-backwards. Palpebral furrow follows change of curvature of palpebral lobe with a somewhat angulate bend. Palpebral furrow is deep but at anterior end it terminates at a poorly defined eye ridge. Intraocular cheek very slightly convex. Posterior border not clearly preserved on available material. Glabella smooth, scattered punctae on cheeks.

Small, wide pygidium is attributed to this species. Wide axis tapers posteriorly and terminal piece merges with a deep, steeply downsloping posterior border, the outline of which is transverse medially. Two axial rings are completely defined, a third faintly. Similarly, two segments are defined on the narrow (tr.) pleural fields, with pleural and interpleural furrows about equally incised, with a short, faint pleural furrow of a third segment.

Discussion. This species differs from the type species of *Phorocephala*, *P. typa* Lu, 1965 (pl. 123, fig. 14; 1975, pl. 34, fig. 13) in its parabolic glabella and punctate (rather than pustulose) surface sculpture; the palpebral lobes of *P. typa* are less curved. Our species has a glabellar form like that of *G. prima* Ross, 1951 (pl. 18, fig. 17), which is primitive for the Telephinidae. The curvature of the palpebral lobes is also reminiscent of *Goniophrys*. On the other hand, the wide, transverse cranidial anterior border precludes its inclusion in that genus and clearly allies it with *Phorocephala*. The glabella and palpebral lobes are primitive characters retained from a *Goniophrys*-like ancestor, which is in accord with the early stratigraphic occurrence of our species compared with that of other described *Phorocephala* (= *Carrickia*) spp. The closest comparison is with *P. genalata* Lu, 1975 from a late Arenig occurrence in south-west China, which has a similar glabella. Unfortunately it is described from poor material: the preglabellar field appears to be longer, and the intraocular cheeks are wider than in our species. *Goniophrys* (sic.) *venustus* Ancign, 1977 (pp. 70–71, pl. 1, figs. 14–20, 24), from the early Ordovician, Karakol–Mikailov Formation of the southern Urals, differs from our species in its very wide glabella, and broad, flattened border on the pygidium. Although ours is therefore apparently a new species, the material is insufficient to name it as such—hence our comparative reference to *P. genalata*. One Llanvirn species with punctate sculpture is that referred by Whitington (1965) to *Goniophrys breviceps*? (Billings) from the Llanvirn of Newfoundland; this species is also referable to *Phorocephala*. The very long palpebral lobes and convex cranidial border immediately distinguish it from our species.

Genus *Carolinites* Kobayashi, 1940

Type species. *Carolinites bulbosus* Kobayashi, 1940, by original designation.

Discussion. The morphology of *Carolinites* is now well-known from a number of species, and the stratigraphic importance of the genus is established. It is unfortunate that the type species, *C. bulbosus*, has not been redescribed from topotype collections. As interpreted by Legg (1976) from Canning Basin material, *C. bulbosus* would be the senior synonym of the widespread species *C. genacinaca* Ross, 1951. Legg's specimens are undoubtedly conspecific with the species from North America, but it is less clear that this applies also to the type material of *C. bulbosus*. The width of the fixed cheek (Kobayashi 1940, pl. 12, fig. 6) adjacent to the baccula, for example, is less than in typical specimens of *C. g. genacinaca*, and belongs to the range of overlap between that species and *C. ekphymosus* Fortey, 1975 (text-fig. 14; pl. 39, figs. 4, 10), a species which is probably a senior synonym of *C. pardensis* Legg, 1976. However, the pygidium, possibly incorrectly assigned to *C. bulbosus* by Kobayashi, is unlike that of any other *Carolinites* species, being relatively transverse, and with a flattened border. In view of these uncertainties we prefer to compare our material with previously described species for which cranidium, pygidium and free cheek are known.

Carolinites genacinaca Ross, 1951 (s.l.)

Plate 45, figs. 7–10

Synonymy. Synonymy of this species, and its two subspecies, was given by Fortey (1975; 1980a, pp. 103, 104).

Material. Cranidia, CPC 22728, 22729; pygidia, CPC 22726, 22727.

Occurrence. Basal Nora Formation, loc. 071/4.

Discussion. The species is divided into two subspecies: *C. g. genacinaca* Ross, 1951, and *C. g. nevadensis* Hintze, 1953, both known from silicified material. Detailed comparative discussion of these subspecies was given by Fortey (1975). A crucial point of distinction is the presence of a marked subocular ridge in *C. g. nevadensis*. We do not have a free cheek from the Nora Formation which might show this feature, and so we prefer to identify the species *sensu lato*. That apart, the relative size of the bacculae adjacent to the base of the glabella, and the clear definition of the third pygidial axial ring shown by the Australian material, are features of the subspecies *C. g. genacinaca*, a mid-Arenig form.

The type specimen of *C. minor* (Sun, 1931) was re-illustrated by Lu (1975, pl. 2, fig. 20); it is very like cranidia of *C. genacinaca* of the same small size. *C. minor* may prove to be the senior synonym both of *C. genacinaca* and *C. bulbosus*, but in view of the uncertainty surrounding the identity of the type species, we employ the well-characterized species *C. genacinaca* here.

Carolinites cf. *C. ekphymosus* Fortey, 1975

Plate 45, figs. 11–14

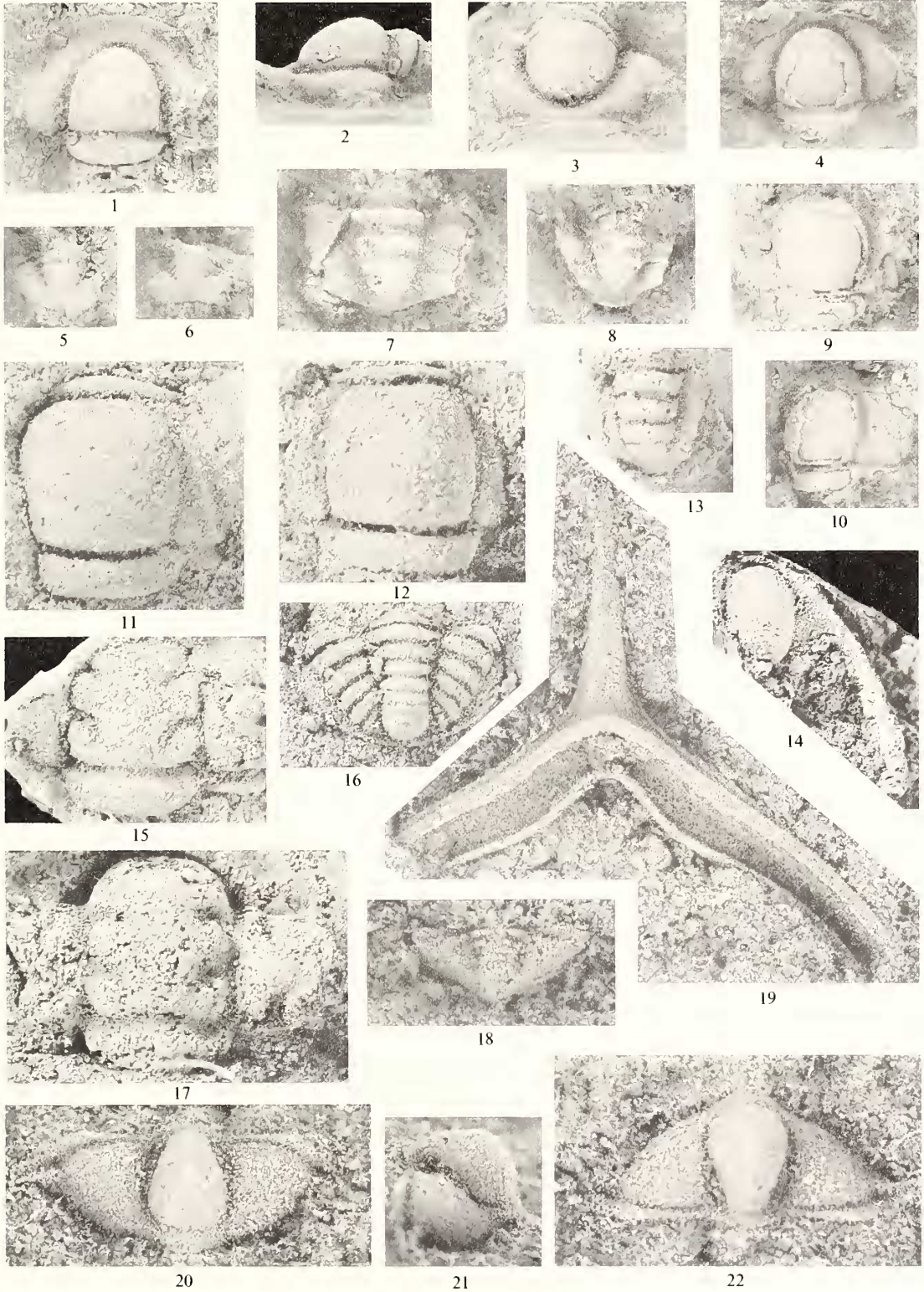
Material. Cranidia, CPC 22732–22740, 22916–22930; librigenae, CPC 22748–22750; pygidia, CPC 22741–22747, 22931–22942.

Occurrence. Ranges through much of the higher part of the Nora Formation, locs. 118/7, 122/4, 126/3, 126/4, 158/4, 308/1.

Discussion. This species of *Carolinites* with narrow fixed cheeks is mostly represented by poorly preserved external moulds, but a few good specimens allow comparison with previously described species. Narrow-cheeked *Carolinites* include *C. sibiricus* Chugaeva, 1964 (= *C. angustagena* Ross, 1967) and *C. ekphymosus* Fortey, 1975 (= *C. pardensis* Legg, 1976, see Fortey 1980a, p. 104). The former has the genal spine reduced to a small stub, whereas the Nora species has a well-developed and curved genal spine. This is like *C. ekphymosus* from the late Arenig of Spitsbergen (Fortey 1975, pl. 39, fig. 2). Well-preserved Nora cranidia are also very like those of *C. ekphymosus* (compare Pl. 45, fig. 11 with Fortey 1975, pl. 39, fig. 3). One of the characteristics of *C. ekphymosus* is a finely granulate surface sculpture, and none of the Australian material is well enough preserved to show this. The pygidia of *C. ekphymosus* from Spitsbergen show a faintly defined fourth axial ring on the pygidium,

EXPLANATION OF PLATE 45

- Figs. 1–6. *Phorocephala* sp. aff. *P. genalata* Lu, 1975. All from Nora Formation, loc. 071/4. 1–3, CPC 22722, exfoliated cranidium in dorsal (1), lateral (2), and anterior (3) views, $\times 8$. 4, CPC 22723, cranidium, $\times 8$. 5, 6, CPC 22725, pygidium, dorsal (5) and posterior (6) views, $\times 8$.
- Figs. 7–10. *Carolinites genacinaca* Ross, 1951 (s.l.). All from lowest Nora Formation, loc. 071/4. 7, CPC 22726, pygidium, $\times 6$. 8, CPC 22727, pygidium, $\times 6$. 9, CPC 22728, incomplete cranidium, $\times 6$. 10, CPC 22729, small cranidium with well-preserved cheek on right side showing relatively great width compared with *C. cf. ekphymosus*, $\times 6$.
- Figs. 11–14. *Carolinites* cf. *C. ekphymosus* Fortey, 1975. 11, CPC 22732, loc. 118/7, cast of cranidium, $\times 6$. 12, CPC 22733, loc. 308/1, cast of cranidium with narrowest cheeks, $\times 7$. 13, CPC 22741, loc. 308/1, cast of pygidium, $\times 6$. 14, CPC 22748, loc. 308/1, free cheek, latex cast, $\times 6$.
- Figs. 15–17. *Annamitella brachyops* sp. nov. 15, CPC 22773, loc. 308/1, latex cast of incomplete cranidium showing granulose sculpture, $\times 4$. 16, CPC 22774, loc. 308/1, pygidium, $\times 6$. 17, CPC 22772, loc. 308/1, holotype, internal mould of cranidium in typical preservation, $\times 6$.
- Figs. 18–22. *Nambeetella embolion* sp. nov. 18, CPC 22757, loc. 126/7, pygidium, internal mould, $\times 6$. 19, CPC 22755, loc. 126/3, cephalic doublure with median spine, same bed as holotype, $\times 6$. 20–22, CPC 22751, loc. 126/3, holotype, latex cast of external mould of cranidium, in anterior (20), lateral (21), and dorsal (22) views, $\times 6$.



FORTEY and SHERGOLD, Nora Formation trilobites

which we have not seen on Australian specimens. These small differences could be because of preservation, but it is preferable to retain a qualification in the determination. Narrowest-cheeked specimens from the Nora Formation (Pl. 45, fig. 12) are like *C. sibiricus*, but no associated free cheek that we have prepared has the genal spine reduced, and the fourth pygidial axial ring is clearly defined on *C. sibiricus*. Regardless of specific identity no *Carolinites* with large bacculae but narrow fixed cheeks is known elsewhere before the later Arenig.

Family ALSATASPIDIDAE Turner, 1940

Emended diagnosis. Trinucleine trilobites in which the median cephalic spine originates from the cephalic doublure. Eyes present primitively; later forms blind. Some forms tend to multiplication of thoracic segments (probably to as many as thirty in *Seleneceme*).

Discussion. Fortey (1975, p. 92) noted the difficulties in an objective definition of this family. We now believe that the presence of a long anterior spine, originating from the cephalic doublure (rather than the glabella as in raphiophorids), is a shared, derived character unusual enough to indicate a monophyletic group. As thus recognized, the Alsataspididae would include *Seleneceme*, *Falanaspis*, *Nambeetella* (below), and '*Hapalopleura*' *longicornis* Harrington and Leanza, 1957. As Fortey noted, the reconstructions of the first- and last-named given in the *Treatise* (Moore 1959) are incorrect in showing what appears to be a dorsal origin for the frontal spine. Whittard (1958) clearly observed the ventral origin of the frontal spine in *Seleneceme*, while Fortey noted that specimens of '*H*' *longicornis* lacking free cheeks also lacked the frontal spine, which was present on entire specimens. This early Tremadoc species also has small eyes. The implication is that the alsataspidids became blind subsequently. Presumably all trinucleine groups were primitively sighted, and blindness could be polyphyletically derived. *Seleneceme* shows another tendency widespread in raphiophorid-like trilobites—the multiplication of post-cephalic segments. We regard this as an adaptation for life in poorly oxygenated environments (Fortey 1975, p. 93; Fortey and Owens 1978, p. 239), and not of high level taxonomic significance. In support of this is the fact that such highly segmented forms are developed at different times in different groups (*Hapalopleura* in the Tremadoc; *Edmundsouia*, a middle Ordovician raphiophorid; and *Seleneceme*, an alsataspidid).

If this phylogenetic view is correct, there are no grounds for separating the Hapalopleuridae from the Orometopidae (Henningsmoen 1959, p. 170) and the latter family name would take precedence. The extended Orometopidae would embrace primitively sighted genera including the ancestors of raphiophorines and endymioniines. Rushton (1982) has shown the origin of *Myiuda*-like forms from orometopids (in our sense) resembling *Araiopleura*; this shows that *Myiuda* (and *Myindella*), hitherto regarded as comprising a separate family, should be included as a subfamily of Orometopidae.

In summary, we would classify the Trinucleina into the following families: Trinucleidae; Dionididae (syn. Tongxinaspidae Zhou, 1981); Orometopidae (syn. Hapalopleuridae), including Subfamily Myindinae; Alsataspididae; Raphiophoridae (Subfamilies Raphiophorinae, Endymioniinae, and possibly Ampyxinellinae). We are inclined to regard *Eotrinucleus*, the only genus ascribed to the Eotrinucleidae Zhou and Zhang, 1978, as a harpedid.

Genus *Nambeetella* Legg, 1976

Type species. *Nambeetella fitzroyensis* Legg, 1976, by original designation.

Diagnosis. Alsataspidids with convex, flask-shaped glabella not overhanging cranidial margin. Triangular pygidium with one or two pairs of pleural furrows.

Discussion. The use here of Legg's genus *Nambeetella* requires some justification. Legg did not describe the free cheeks of the type species, and the free cheeks include the critical alsataspidid feature of the anteromedian spine. The cranidium alone is extremely like that of *Globampyx trinucleoides* Fortey (1975, pl. 29, fig. 1) from the Arenig of Spitsbergen, but this is a raphiophorine entirely lacking a frontal median spine. Legg (1976) compared *Nambeetella* with *Mendolaspis*, but again this genus appears to have an anterior tubercle on the glabella homologous with the anterior spine of

raphiophorines (Fortey 1975, pl. 30, fig. 8). On our analysis both *Globanpyx* and *Mendolaspis* are raphiophorids, and any resemblance to the alsataspidid from the Nora Formation is a matter of convergence. We have made the assumption, however, that the Nora material and that from the Canning Basin (*N. fitzroyensis*) is congeneric. In view of the other genera in common between the two areas (*Fitzroyaspis*, *Gogoella*, *Prosopiscus*, etc.), and the endemic character of the fauna as a whole, this does not seem an unreasonable assumption. But it requires the discovery of the cephalic doublure of the type species before it can be proven. If the anteromedian spine proved to be lacking on *N. fitzroyensis*, *Nambeetella* would become a junior subjective synonym of *Globanpyx*, and a new generic name would be required for the species described below.

As understood here, *Nambeetella* is distinguished from other genera of the Alsataspididae by its narrow, vaulted glabella and relatively large pygidium; it is the most raphiophorid-like of the family. We regard the presence of the median spine on the doublure as the more reliable indicator of its affinities.

Nambeetella embolion sp. nov.

Plate 45, figs. 18–22

Diagnosis. *Nambeetella* with steeply sloping and somewhat tumid preglabellar field; lateral tips of fixed cheeks extended into spine-like projections. Pygidium about twice as wide as long, with axis occupying about one-third transverse pygidial width at front margin.

Derivation of name. Greek *embolion*, 'javelin', referring to the frontal spine.

Holotype. Cranidium, CPC 22751, from loc. 126/3.

Other material. Cranidia, CPC 22752–22754, 22952, 22953; librigenae, CPC 22755, 22756; pygidium, CPC 22757.

Occurrence. Lower part of Nora Formation, locs. 126/3, 126/4, 126/5, 126/6, 126/7, 127/7.

Description. Cranidia, free cheeks, and pygidium are all from a short stratigraphic interval in which no other trinucleines occur, so their association is made with confidence. Cranidium twice as wide as long, glabella even at maximum width occupying a third cranidial width, or less. Transverse glabellar vaulting increases forwards from quite low near the occipital ring to a maximum at about two-thirds length in dorsal view, in front of which there is a decrease in convexity to the preglabellar furrow. One might expect a tubercle on the anterior high point of the glabella but none is visible—probably the preservation is too coarse to see it. For the same reason no sculptural details are preserved. Two pairs of subcircular muscle impressions on narrow, posterior part of glabella. Fixed cheeks curve downwards progressively forwards, running into the preglabellar field, which protrudes slightly forwards, slopes steeply downwards, and is gently inflated. Axial furrows are quite broad posteriorly but there is no indication of inflated 'alae' within. Short (sag., tr.) anterior cranial border weakly indicated at mid-part of preglabellar field. Well-defined posterior border becomes wider and steeply forwards inclined away from glabella. The most distinctive feature of the cranidium is the prolongation of the borders, and narrow, triangular slivers of the fixed cheeks in front, into curious spine-like projections at the posterolateral corners of the cranidium.

We have two examples of the cephalic doublure bearing the median spine; all that remains of the dorsal part of the free cheeks is a narrow strip running around the anterior margin of the cranidium. The doublure itself is divided along its length with a somewhat ventrally depressed posterior band, and its inner edge is turned upwards and embayed about the mid-line. The frontal spine tapers from a stout base to reach a length possibly exceeding that of the cranidium; the underside of the spine is flattened near its base, but the cross-section is nearly circular distally. It was probably slightly downward-declined. A curious feature of both specimens is the lack of genal spines. All trinucleines have genal spines, and it seems unlikely that they were absent in *Nambeetella*, but it is difficult to see why they should have been broken off when the anteromedian spine is preserved, particularly in so symmetrical a fashion.

Pygidium twice as wide as long, with steeply downturned posterior border which is not arched up about the mid-line. Gently convex axis occupies about one-third of the pygidial width at the front margin, tapering gently posteriorly, and extends as far as border, but preservation is not good enough to see whether it encroached on to the border in the manner of some raphiophorids. Four narrow axial rings appear to be defined. On the pleural fields only the first pair of pleural furrows are deeply defined. The pygidium is an internal mould, and it is possible that an additional pair of furrows could have been expressed dorsally.

Discussion. The reasons for assigning the species from the Nora Formation to *Nambeetella* have been discussed above. *N. fitzroyensis*, the type and only other species, has a narrower preglabellar field, and Legg (1976) does not mention the distinctive, pointed extensions of the posterolateral angles of the fixed cheeks which are a feature of *N. embolion*. The pygidium assigned to *N. fitzroyensis* is relatively much wider than that of *N. embolion*, with a proportionately narrow axis; a second pleural furrow is defined.

Family PLIOMERIDAE Raymond, 1913

Genus *Gogoella* Legg, 1976

Type species. *Gogoella wadei* Legg, 1976, by original designation.

Gogoella brevis sp. nov.

Plate 46, figs. 11–14; text-fig. 12

Diagnosis. *Gogoella* with glabella wider than long, forward-expanding; fixed cheeks narrow (tr.). Pygidial ribs broad (tr.), steeply downturned, with somewhat truncate spinose tips.

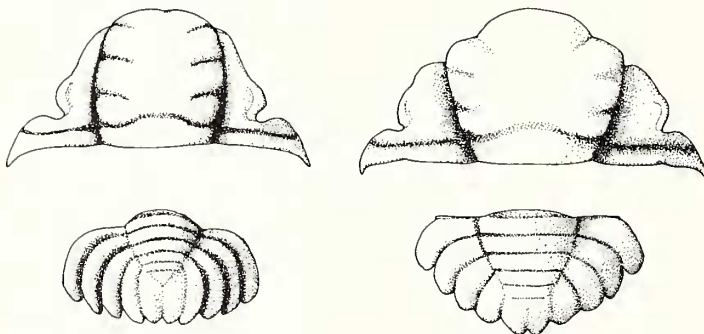
Derivation of name. Latin *brevis*, 'short'.

Holotype. Cranidium, CPC 22758, from loc. 308/1.

Other material. Cranidia, CPC 22954–22956; pygidia, CPC 22759–22761, 22957–22960.

Occurrence. Upper part of Nora Formation, locs. 308/1, 158/4.

Description. A small species, cranidium not exceeding 5 mm in length, but transversely convex. Cranidium with postocular cheeks steeply downturned, glabella squat and flat-topped. Glabella expands forwards so that maximum width is at 3P lobes, this exceeding its sagittal length. Front glabellar margin gently rounded about



TEXT-FIG. 12. Comparative reconstructions of *Gogoella wadei* Legg (left), from the Canning Basin (reconstructed from Legg 1976), and *G. brevis* sp. nov. (right) from the Nora Formation, both about $\times 2$.

EXPLANATION OF PLATE 46

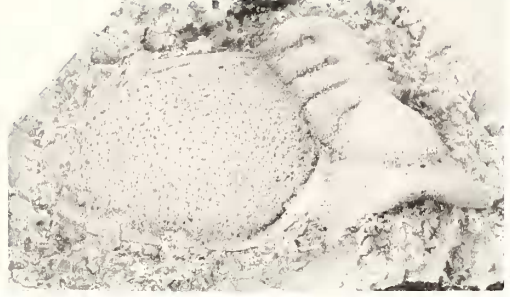
Figs. 1–6, 9. *Prosopiscus praecox* sp. nov. 1, 2, CPC 22762, lower Nora Formation, loc. 071/4, holotype, well-preserved, but broken testate cranidium in dorsal (1) and oblique anterior (2) views, $\times 4$. 3, 5, CPC 22764, loc. 158, latex cast from well-preserved pygidium, dorsal (3) and oblique posterior (5) views, $\times 3$. 4, CPC 22765, loc. 158/9, latex cast from smaller pygidium, $\times 3$. 6, CPC 22766, loc. 158/4, latex cast from pygidium, $\times 5$. 9, CPC 22763, loc. 071/4, incomplete cranidium from same bed as holotype, $\times 6$.

Figs. 7, 8, 10. *Prosopiscus* sp. A. 7, CPC 22767, loc. 071/4, cast from fragmentary, but well-preserved cranidium, $\times 8$. 8, CPC 22768, loc. 308/1, small cranidium, imperfect internal mould, $\times 8$. 10, CPC 22769, loc. 158/9, latex cast from the pygidium most likely to belong here, dorsal view, $\times 3$.

Figs. 11–14. *Gogoella brevis* sp. nov. 11, CPC 22760, loc. 308/1, pygidium, latex cast, showing all five ribs, $\times 6$. 12, CPC 22758, loc. 308/1, holotype cranidium, internal mould, $\times 8$. 13, 14, CPC 22759, loc. 158/4, latex cast from external mould of pygidium, shown in dorsal (13) and posterior (14) views, $\times 6$.



1



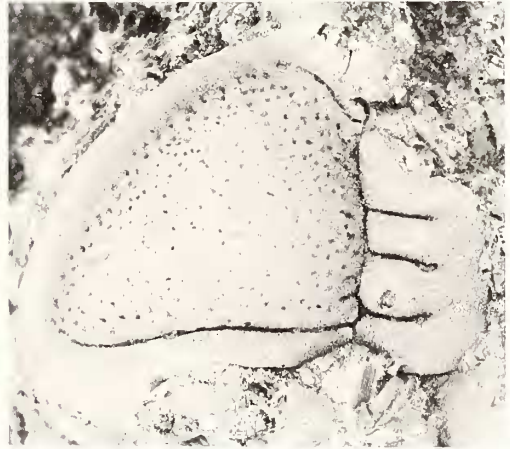
2



3



4



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5



6



8



9



10



11



12



13



14

mid-line. Glabellar expansion is less marked on small cranidia, and the frontal lobe is more broadly rounded. Glabellar furrows short, extending less than one-quarter of transverse glabellar width. 1P deepest, confining narrow (exsag.) 1P lobe; 2P and 3P lobes are progressively longer (exsag.). 2P furrow is directed slightly forwards, approaching axial furrow near its anterior end; 3P directed strongly forwards, finishing well inside the preglabellar furrow. Occipital ring deeply defined, and curving forwards medially. Axial furrows very deep and wide, like posterior border furrow. Because most of our specimens are internal moulds we do not know the dorsal expression of glabellar and other furrows. If they follow the usual pliomerid pattern (pliomerids usually have a very thick cuticle) furrows would have been narrower, but still deep on the dorsal surface. Intraocular cheeks very narrow (tr.) not exceeding one-quarter maximum glabellar width. Palpebral lobes are far back, centred on the 1P glabellar furrow, thereby constricting a narrow (exsag.) and short (tr.) postocular cheek. Anterior border not well-preserved on available material.

Pygidium almost twice as wide as long, pleural ribs deeply downward-curved peripherally. Axis tapers backwards gently and uniformly, the five axial rings decreasing greatly in convexity in the process. The fifth axial ring is incompletely defined posterolaterally. No distinct terminal piece is developed. The pleural ribs are relatively short for a pliomerid, swollen and sausage-shaped, terminating on a line as somewhat truncate-tipped spines.

Discussion. Legg (1976, p. 20) briefly distinguished the type species from other pliomerids; the inclusion of *G. brevis* in the genus modifies the original diagnosis. *G. brevis* differs from *G. wadei* in its forward-expanding and relatively wide glabella, with concomitantly shorter glabellar furrows, 3P being closer to the mid-line in the new species. *G. brevis* has more swollen pygidial pleural ribs than *G. wadei*. Both species share: very narrow fixed cheeks, with the palpebral lobes further back than in any other pliomerid; glabellar furrows similarly disposed, apart from the more adaxial 3P in *G. brevis*; wide pygidium with short ribs (steeply inclined distally, but not extended into long vertical spines). These characters are regarded as important in distinguishing *Gogoella* from other pliomerids. Legg emphasized a small median glabellar indentation on the type species, but this is a character which is widespread in pliomerids—although most strongly expressed in *Pliomera*. Inclusion of *G. brevis* in *Gogoella* means that a 'subelliptical glabella . . . with anterior furrow approximately at anterolateral angle of glabella' (Legg 1976, p. 19) cannot be used to distinguish the genus from *Pliomera*. The type species of that genus, *P. fischeri* (e.g. Neben and Krueger 1975, pl. 10, figs. 18–20), is more like *G. brevis* than *G. wadei*, but in *P. fischeri* the median cephalic indentation is developed as strongly as the (very short) 3P glabellar furrows, the palpebral lobes are further forward, and, as Legg pointed out, the structure of the cranidial anterior border is quite different from that in *G. wadei*. The long (sag.) pygidium of *P. fischeri* is unlike that of *Gogoella*. We regard the cephalic similarities between *Gogoella* and *Pliomera* to be the result of convergence. Similarly, on *Pliomerops canadensis* (see Shaw 1968, pl. 1, fig. 4) the 3P glabellar furrows are far forwards, as in *G. brevis*, but the structure of the pygidium, with long, downturned spines, is quite different from the Australian forms. It seems that the anterior, adaxial migration of the 3P glabellar furrows is an evolutionary trend in pliomerids that was attained independently several times.

Legg (1976) reported only ten thoracic segments on *G. wadei*, the smallest number of any pliomerid known to us. The structure of the anterior border of this species is also unusual in the Pliomeridae, being thin and almost tucked beneath the frontal glabellar lobe. We lack information on the border structure of *G. brevis*, however.

Family PROSOPISCIDAE fam. nov.

Diagnosis. Blind Phacopina with broad, convex fixed cheeks covered with pitting. Glabella typically tapering in later species, but primitively subparallel sided. Broad anterior cranidial border, often sloping back towards glabella. Eye ridges running immediately forward from 3P glabellar furrow to margin on primitive forms. Pygidium with six to eight segments, equally developed pleural and interpleural furrows; posterior pleural bands tending to fuse with border.

Discussion. *Prosopiscus* is the only genus assigned to the new family; it has hitherto been placed with the Encrinuridae or Cheiruridae. Our reasons for regarding it as a separate family are given with a discussion of its affinities in the following paragraphs.

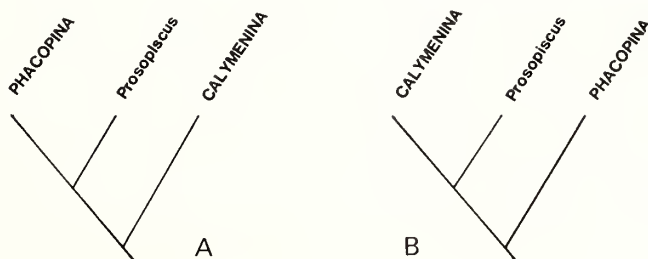
Genus *Prosopiscus* Salter, 1865

Type species. *Prosopiscus minus* Salter, 1865, by original designation.

Discussion. The Nora Formation has yielded good material of this most extraordinary trilobite. The genus has hitherto been recorded from rocks of Llanvirn to Caradoc age; our species are therefore by far the oldest, and are appropriate for a consideration of the affinities of the genus. Lu (1975) discussed *Prosopiscus* at some length, and described well-preserved cephalic shields of three Chinese species. He concluded that the genus should be assigned to the Family Cheiruridae, Subfamily Areiinae Prantl and Přibyl. Lu and Chang (1974) figured a complete specimen of *P. latus*. We have also attributed the pygidium here, and this rules out any possibility of cheirurid affinities for *Prosopiscus* because the pygidium has up to eight segments, and an entire margin. The resemblance to *Areia* must be a matter of convergence. However, several features, particularly the pitted sculpture on the fixed cheeks and the form of the glabellar furrows, show that whatever its closest relatives *Prosopiscus* belongs to the Order Phacopida. The genus had a history extending through much of the Ordovician, and its earliest representatives are as old as any dalmanitacean, for example. In view of its curious combination of characters, and this long independent history, we regard *Prosopiscus* as belonging to a distinct family.

To which of the major groups of Phacopida is *Prosopiscus* most closely allied? We presume that the Cheirurina can be excluded, because of the entire pygidial margin of *Prosopiscus*, with the pleural ribs bisected by long, deep pleural furrows. This leaves two possibilities (A and B in text-fig. 13): *Prosopiscus* is more closely related to the Phacopina than the Calymenina, or vice versa. Blindness as a character is irrelevant, because it is capable of polyphyletic development. Later species of *Prosopiscus* have a markedly forward-tapering glabella, but this is not the primitive condition; our early species has a parallel-sided glabella, or even with slight expansion at the 3P glabellar lobe, and it is this form which must be compared with phacopines and calymenines. The ocular ridge is strongly defined, running forwards from the 3P glabellar furrow to the cranial margin. The anterolateral view of the specimen of *P. praecox* on Plate 46, fig. 2, shows that there was room for a minute, triangular free cheek adjacent to the cranial anterior border. However, the fact that no palpebral lobe is developed makes it very unlikely that there was even a rudimentary eye. The interpretation of the facial suture presents several problems. If a free cheek were present, then what appears to be the edge of the lateral cranial border is interpretable as a suture which may run some way towards the genal angle. In support of this interpretation is the fact that the anterior cranial border is distinctly rolled back into the doublure, whereas the 'border' on the fixed cheek is much narrower, not rolled and sharply truncated at its edge. The free cheek would then consist of the outer part of the border plus doublure. However, on species with broad lateral cranial borders (Pl. 46, fig. 7, and those in Lu 1975) the suture has presumably retreated to a completely marginal position, and this applies to all the younger species.

Of derived characters which might indicate calymenine affinities, one only is considered important: the structure of the anterior cranial border, which is robust, convex-forwards, and increases in width (tr.) away from the glabella. It may be compared with the structure of the preglabellar area of such early calymenids as *Neseuretus*. Although the tapering glabellae of calymenines and most



TEXT-FIG. 13. The two competing hypotheses for the closest related taxa to the peculiar trilobite *Prosopiscus*, as discussed in text.

Prosopiscus spp. are similar, this is clearly a secondary character in the latter, the primitive glabellar form being parallel-sided. The pygidium cannot be closely matched among calymenids, although some *Platycalymene* species are not dissimilar in general structure.

Derived characters which might indicate Phacopina are as follows: (1) The finely pitted surface sculpture on the fixed cheeks; such a sculptural type is present on many early Phacopina (Destombes 1972, pl. 4, fig. 1; Henry 1980, pl. 28, fig. 5b), while calymenids are apparently primitively granulate. (2) The form of the 3P glabellar furrow is typically phacopinoid, showing gently sigmoidal curvature and much greater forward inclination than the 2P furrow, making the 3L glabellar lobe longest (exsag.). (3) The pygidium is most like that of *Eudolaites* among phacopines (see *E. (Banilatites)* aff. *dubius* figured by Destombes 1972, pl. 4, fig. 7) with regard to the development of pleural and interpleural furrows, and the retention of relict half-rings on the pygidial axis.

We conclude that more derived characters indicate the common ancestry of *Prosopiscus* and Phacopina than Calymenina. Pygidial details show that the Dalmanitidae include the closest forms. Since both *Prosopiscus* and Dalmanitidae are found in the Arenig, their common ancestor is of Tremadoc age or older but we know of no suitable candidate. The early origin and subsequent history of *Prosopiscus* indicates that its familial status is justified.

Note that other phacopids became blind: *Typhloniscus* is a Devonian genus which is homoeomorphic in some respects with *Prosopiscus* (Rennie 1930, pl. 10, fig. 12). In its glabellar furrows and pygidial features *Typhloniscus* is clearly a phacopid derivative, and there is no question of classifying it with *Prosopiscus*. It is interesting to observe, though, that the manner of eye loss appears to have been similar in both genera: forward migration of the facial sutures and (presumably) eventual elimination of the ocular part of the fixed cheek. *Areia* in the Cheiruridae may have lost its eyes in the same way.

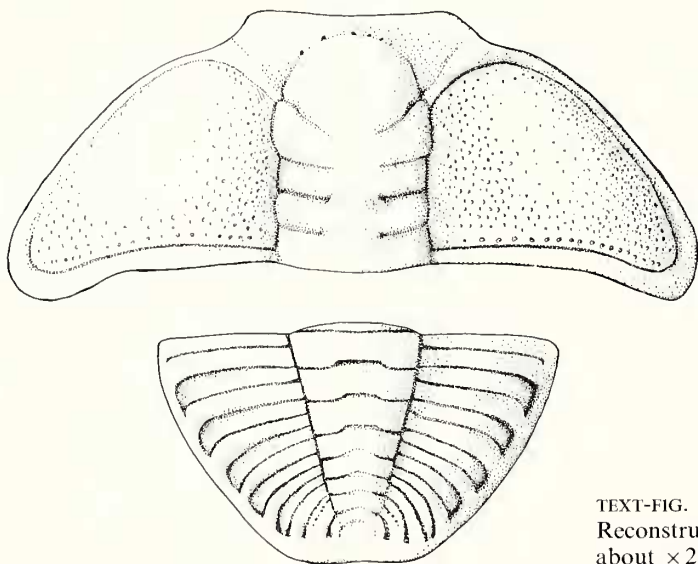
Prosopiscus praecox sp. nov.

Plate 46, figs. 1-6, 9; text-fig. 14

Diagnosis. *Prosopiscus* with glabella nearly parallel-sided; remnant eye ridges present; lateral border narrower than other species. Genal pitting very dense.

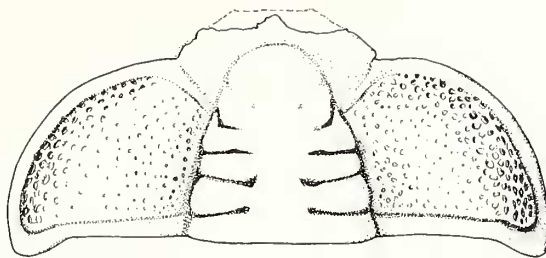
Derivation of name. Latin *praecox*, 'Spring', referring to its early appearance in the Nora Formation.

Holotype. Cranium, CPC 22762, from loc. 071/4.



TEXT-FIG. 14. *Prosopiscus praecox* sp. nov.
Reconstruction of cephalon and pygidium,
about $\times 2$.

TEXT-FIG. 15. *Prosopiscus minus* Salter. Reconstruction of the cephalon of the type species of *Prosopiscus*, based on fragments in the type collection in the British Museum (Natural History), about $\times 2$.



Other material. Cranidium, CPC 22763; pygidia, CPC 22764–22766, 22961.

Occurrence. Throughout most of Nora Formation, from locs. 071/4, 158/4, 158/9, 158/11.

Description. Cranidium deeply vaulted transversely, with lateral parts of cheeks steeply downslowing, and broad arch about the mid-line. Cheeks about one and a half times the maximum width of glabella, which is elevated above the cheeks rather than sunk between them, as in species such as *P. rugosus* Lu. Glabella almost parallel-sided, though with a tendency for the 3L lobe to bulge outwards slightly into axial furrow; frontal lobe with semicircular outline. First pair of furrows on glabella interpreted as lateral parts of occipital furrow, very shallow over mid-part of axis. Lateral glabellar furrows likewise extend far into glabella, defining a median glabellar lobe only about one-quarter width of glabella. 1P and 2P transverse (inner end of 1P deepened into an apodeme), glabellar lobe 2L slightly shorter (exsag.) than 1L. 3L is longer than either, adjacent to axial furrow, slightly inflated, delimited by 3P furrow which slopes inwards quite strongly, and is gently sigmoidal. Axial and preglabellar furrows nowhere deep, except for hypostomal pit, but there are four or five pits in the preglabellar furrow. Eye ridge almost continuing line of 3P glabellar furrow, furrow defining its posterior edge much the deeper, and continuing without a break into lateral border furrow. Although the eye ridge is slightly wider where it joins the border there is no palpebral lobe. Area in front of eye ridge continuous with cranial anterior border (although the posterior part may well have a genal origin), which is narrowest medially and broadly 'rolled'. Anterior view shows a short section (Pl. 46, fig. 2) of the presumed facial suture terminating the anterolateral edge of the border. The question of whether a free cheek was present, and its probable extent, has been touched upon above. Lateral border narrow, no wider than the eye ridge; posterior border about twice as wide as lateral; genal angle rounded. Borders appear to lack the dense granulation that occurs everywhere else. Cheeks alone are densely pitted; the largest pits are concentrated in a line of about fifteen pits a little in front of the very narrow posterior border furrow.

Pygidia assigned here are two-thirds as long as wide, with slightly elevated axis, and distal part of pleural fields deeply downslowing. External mould shows seven segments clearly defined, and an eighth only indicated. Axis tapers gently almost to border, with seven rings and a small terminal piece. Long, narrow pleural furrows divide each segment into anterior and posterior bands, of which the anterior only merges with the slightly convex border. Posterior bands are sharply marked off from border by deep furrows. Narrow border widens and becomes more rounded where arched upward about mid-line. Internal moulds show that doublure was ventrally correspondent with border, forming marginal tube, widest posteriorly.

Discussion. The type species of *Prosopiscus*, *P. minus*, was redescribed by Reed (1912); the type material is fragmentary. We have used it as the basis for a new reconstruction shown in text-fig. 15. Compared with *P. praecox*, the borders are much wider and the glabella tapers strongly, differences which also apply to the several younger species figured by Lu (1975). The closest species is *P. edgarensis* Legg, 1976 (pl. 6, figs. 30, 35) from the early Llanvirn of the Canning Basin, north-western Australia. The specimens used to found this species are small and flattened, hence comparison is difficult with our material, but several differences are shown, not all accountable to preservation or size. The posterior border furrow of *P. edgarensis* is comparatively deep and wide, while the genal pitting is coarse. No lateral border is shown on the cranidia figured by Legg and according to him the border on this species is entirely librigenal: free cheeks 'narrow (tr.) and almost entirely consist of border only' (ibid., p. 23). *P. latus* Lu, in Lu and Chang 1974 from the late Arenig of south-west China, has a broad lateral cephalic border, and an acutely triangular pygidium with feeble interpleural furrows.

Our assignment of the pygidium to *P. praecox* is based on the following assumptions: having matched other pygidia and cranidia in the fauna, we were left with two kinds of *Prosopiscus* cranidia, and two types of pygidia, in approximately equal abundance scattered through the Nora Formation; the assumption that they belonged together seems reasonable. On morphology the assignment is consistent: low axial convexity is matched by glabella and pygidial axis, *P. praecox* has nearly horizontal fixigenal areas adaxially, distally turning downwards steeply, a profile which must have been reflected in the thorax, and which is shown also on the pygidium we assign to *P. praecox*. Note also that the axial arch along the mid-line is similar on cranidium and pygidium of *P. praecox*, and that the 'thickened' appearance of the anterior cranial border is matched also by the adaxial part of the pygidial border. The longer of the two types of pygidia was assigned to *P. praecox* because of its convexity and relatively narrow border; the wider type of pygidium was matched with *P. sp. A* (below), which is less convex, and with broad borders. Both are also generally similar to the pygidium in the complete specimen of *P. latus* Lu, in Lu and Chang 1974 (pl. 51, fig. 10).

Prosopiscus sp. A

Plate 46, figs. 7, 8, 10

Material. Cephalic shields, CPC 22767, 22768, 22962, 22963; pygidia, CPC 22769–22771, 22964–22966.

Occurrence. Nora Formation, locs. 071/4, 158/9, 308/1.

Discussion. Cephalic material of this species is insufficient to formally name it as new. It obviously differs from *P. praecox* in the following respects: (1) Lateral cephalic border is very broad; there is no question here of a narrow librigenal strip appearing dorsally and if there were any librigenal remnant it would have to be wholly ventral; overall cephalic convexity is lower than that of *P. praecox*. (2) Fixigenal pitting has about half the density of that on *P. praecox*; pits become large and sparse near lateral border. (3) Length (exsag.) of 2P glabellar lobe is relatively short in relation to 1P and 3P. (4) The pygidium is much more transverse and less convex than that assigned to *P. praecox*; only four (faint fifth) axial rings are present; pygidial pleural regions are greatly effaced compared with *P. praecox* and only the anterior segment is clearly defined. None the less the basic similarity of construction of the pygidia of the two species is apparent in the form of the borders and axial rings; internal moulds of pygidia of *P. sp. A* show similar pleural morphology to that observed on *P. praecox* dorsally.

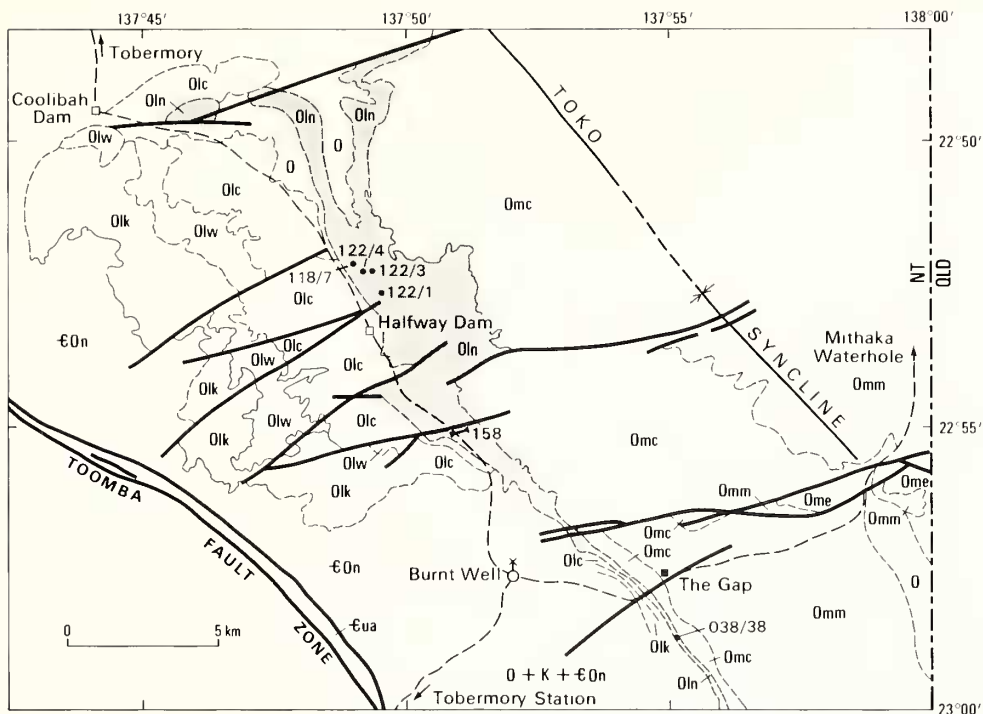
LOCALITY INFORMATION

Material described here has been collected from both single samples and measured sections, principally on the Toko, Abudda Lakes, and Mount Whelan 1:100 000 Geological Series Sheets, numbers 6452, 6551, and 6651, respectively. These sheets form portions of the Tobermory and Mount Whelan 1:250 000 Geological Series Sheets, SF/53-12 and SF/54-13, respectively. Localities are given grid references from the 1:100 000 scale series, and additional geographic references for location where only 1:250 000 scale sheets are available. They are listed numerically.

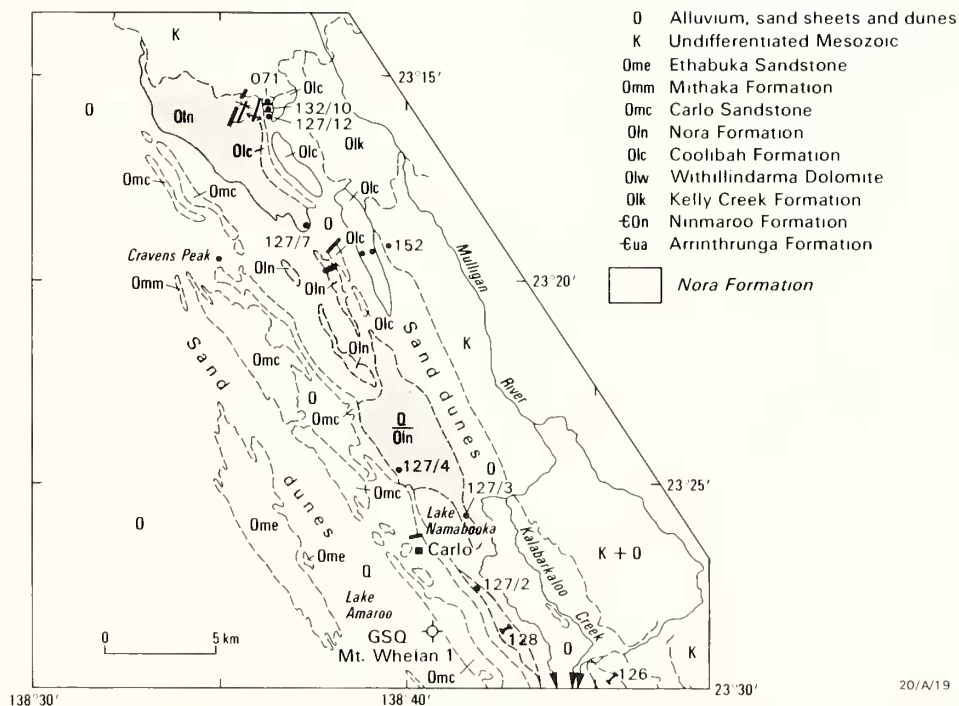
Locality 015/6: this refers to Stop 15 on the 1976 International Geological Congress field Excursion 4C (Shergold *et al.* 1976, p. 25, fig. 13), and is referred to more fully under Section 158 below. Samples numbered 015/6, 158/4, and 308/1 are all from the same layer.

Locality 038/38: specimens prefixed 038 are from spot sampling on the Toko and Neeyamba Hill 1:100 000 Geological Sheets 6452 and 6552, respectively. Sample 038/38 (text-fig. 16) is on the Toko Sheet at grid reference 79950 74563, geographic coordinates lat. 22°58'24" S. and long. 137°55'10" E., 6 km ESE of Burnt Well and 1.5 km SSE of The Gap Outstation. Brachiopods, bivalves, and gastropods occur with *Presbynileus* cf. *P. utahensis* in quartz sandstones from the upper part of the Nora Formation.

Section 071: Syncline (text-fig. 17), 14.5 km WSW of Rocky Waterhole, and 7.5 km due N. of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet, grid reference 25500 74256, geographic coordinates lat. 23°15'34" S., long. 138°36'19" E., containing a short sequence at the boundary between Coolibah Limestone and Nora Formation. At this locality the basal Nora Formation comprises poorly outcropping coarse pebbly



TEXT-FIG. 16. Detailed locality map for the Nora Formation in the Toko syncline.
For key see text-fig. 17 below.



TEXT-FIG. 17. Detailed locality map for the Nora Formation in the Carlo-Cravens Peak district.

skeletal grainstone layers, interbedded with fine sandstone and siltstone, and generally concealed below alluvium. The following trilobite fauna occurs with gastropods, rostroconchs, bivalves, nautiloids, ostracodes, and an eocrinoid: *Amamitella strigifrons*, *Carolinites genacinaca*, *Prosopiscus praecox*, *P. sp. A.*, *Norasaphus* (*Norasaphus*) *skalís*, *Lycophron* sp. A., *Phorocephala* sp. aff. *P. genalata*, and *Hungioides acutinasus*.

Section 118: 25 m sequence of fossiliferous grainstone overlain by fine-grained sandstone, 2 km N. of Halfway Dam, Toko Range 1:100 000 Sheet area. Horizon 118/7: sandstone containing *L. rex*, *C. cf. ekphymosus* (text-fig. 16), lying 21.5 m above base of section at geographic coordinates lat. 22°51'28" S., long. 137°48'46" E., lower part of Nora Formation.

Localities 122/1, 122/3, and 122/4 (text-fig. 16) refer to spot samples taken in the vicinity of Halfway Dam on the Toko 1:100 000 Sheet (text-fig. 16). 122/1 is 1.10 km ENE of Halfway Dam at grid reference 78980 74672, and geographic coordinates lat. 22°52'37" S., long. 137°49'29" E. 122/3 is 1.7 km N. of Halfway Dam at 78960 74679, lat. 22°52'23" S., long. 137°49'2" E. 122/4 is 1.8 km N. of Halfway Dam at 78920 74679, lat. 22°52'28" S., long. 137°48'42" E. Fine-grained sandstones occur at all three localities in the lower part of the Nora Formation, and these contain brachiopods, gastropods, nautiloids, and bivalves, together with *L. rex* (122/1, 122/3), *Fitzroyaspis irritans* (122/4), *N. (Norasaphites) monrocae* (122/1?), *N. (N.) vesiculosus* (122/1, 122/4), and *H. acutinasus* (122/1).

Section 126: this section (text-fig. 17) is located 10.5 km SE of Carlo Homestead, at grid reference 27110 73999 and geographic coordinates lat. 23°29'31" S., long. 138°45'20" E., on the Mount Whelan 1:100 000 Sheet. Some 20 m of varicoloured siltstone and sandstone layers are separated by intervals of no outcrop. Stratigraphically, the section is thought to lie slightly above that exposed at 071. Nautiloids, bivalves, brachiopods, ostracodes, and ichnofossils are associated with *L. rex* (126/1, 126/2, 126/3, 126/5), *H. acutinasus* (126/1, 126/3, 126/4, 126/5, 126/11), *A. strigifrons* (126/3), *C. cf. C. ekphymosus* (126/3, 126/4), *Nambeetella embolion* (126/3, 126/4, 126/5, 126/6, 126/7), *Presbynikleus* cf. *P. utahensis* (126/7), *F. irritans* (126/7), and *Norasaphus* (*Norasaphites*) *vesiculosus* (126/1, 126/2, 126/3, 126/4, 126/5, 126/6, 126/7, 126/11).

Localities prefixed 127 refer to spot samples collected along the length of the Toomba Range and western portion of the Toko Syncline.

127/2: spot sample located immediately S. of Lake Namabooka, 3 km SE of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26450 74040, geographic coordinates lat. 23°27'30" S., long. 138°41'42" E. Fine-grained sandstone has yielded bivalves and *N. (Norasaphus) skalís*.

127/3: sample collected on eastern side of Lake Namabooka, 1.9 km NE of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26370 74070, geographic coordinates lat. 23°25'45" S., long. 138°41'8" E. Fine-grained sandstone contains ichnofossils and *Phorocephala* sp. aff. *P. genalata*.

127/4: locality situated approximately 3 km N. of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26110 74090, geographic coordinates lat. 23°16'30" S., long. 138°39'55" E. Fine-grained sandstone contains ichnofossils and *N. (N.) skalís*.

127/7: a spot sample 4.4 km NE of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, at grid reference 25700 74200, geographic coordinates lat. 23°18'35" S., long. 138°37'22" E. The locality contains a sequence of sandstone with calcareous lenses in the lower part of the Nora Formation. Ostracodes and bivalves occur with *L. rex* and *Nambeetella embolion*, and the conodonts *Trigonodus* and *Drepanoistodus* spp.

127/12: this locality is adjacent to 132/10 at the southern end of the synclinal structure 1 km S. of section 071, at grid reference 25500 74250, geographic coordinates lat. 23°16'18" S., long. 138°36'30" E. (text-fig. 17), Mount Whelan 1:100 000 Sheet area. Varyingly indurated, lateritized sandstone, siltstone, and carbonate occurs at these localities. Nautiloids and a bivalve are associated with *L. rex* and *Norasaphus* (*Norasaphus*) *skalís*.

127/15: spot sample at S. end of Ilanama Swamp, 21.5 km NW of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 24520 74387, geographic coordinates lat. 23°8'22" S., long. 138°30'41" E. Fine-grained sandstone contains ichnofossils, brachiopods, nautiloids, and *N. (N.) skalís*.

Locality 132/10: see 127/12 (above).

Locality 139/4: this locality lies at the SE corner of Ilanama Swamp, 22.3 km NNW of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, at grid reference 24550 74394, geographic coordinates lat. 23°8'0" S., long. 138°30'55" E. A skeletal, peloidal clast grainstone sequence about 10 m thick, contains brachiopods, bivalves, and *N. (Norasaphites) vesiculosus*.

Section 152: this is a long and discontinuous line of section running from the top of the Kelly Creek Formation (152/1) into the lower Nora Formation (152/10), commencing 7.5 km due east of Cravens Peak outstation and terminating 4.2 km from the same (text-fig. 17), on the Mount Whelan 1:100 000 Sheet, grid reference 26050 74192 to 25770 74180, geographic coordinates for 152/9, lat. 23°19'37" S., long. 138°37'55" E. Locality

152/9 comprises varying indurated micaceous sandstone containing bivalves, nautiloids, and brachiopods associated with *L. rex* and *H. acutinasus*, and two species of the conodont *Trigonodus*.

Section 156: this section line runs from the Coolibah to the Nora Formation, commencing 7.5 km WSW of Mount Harriet on the Abudda Lakes 1:100 000 Sheet area, grid references 20350 74176 to 20280 74177, and geographic coordinates approximately lat. 23°19'23" S., long. 138°5'40" E. to lat. 23°19'28" S., long. 138°6'4" E. Nora Formation comprises some 42 m of quartz sandstone and skeletal pelletal grainstone yielding brachiopods and *N. (N.) vesiculosus* throughout.

Section 158: this section (text-fig. 16) was initially spot sampled and the numbers 308/1, 308/2, and 015 also refer to it. Section 158 is located 5 km NNW of Burnt Well, and 8.5 km NW of The Gap outstation in the Toko 1:100 000 Sheet area, grid references 79180 74625 to 79420 74625, and geographic coordinates lat. 22°55'8" S., long. 137°50'43" E. to lat. 22°55'5" S., long. 137°51'2" E. The section (see also Shergold *et al.* 1976, p. 25, fig. 13) exposes some 26 m of resistant ferruginized carbonate layers significantly devoid of trilobites, overlain by a further 30–40 m of flaggy bedded sandstone and siltstone with occasionally more calcareous interlayers, now decalcified, which contain the richest faunas (e.g. horizon 158/4, = 308/1, = 015/6). These sandstones represent the lower portion of the upper Nora Formation. A variety of molluscs, bivalves, gastropods, a rostroconch, and brachiopods occur on section 158. Trilobites, occurring in the interval between 26–40 m, include *A. brachyops*, *C. cf. C. ekphymosus*, *F. irritans*, *Gogoella brevis*, *H. acutinasus*, *L. rex*, *N. (N.) monroae*, *N. (N.) vesiculosus*, *Presbynilus cf. P. utahensis*, *Prosopiscus praecox*, and *P. sp. A*.

Localities 308/1 and 308/2: see section 158 (text-fig. 16) above.

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